

By Laurence M. Klauber

IV THE GROWTH OF THE RATTLESNAKE

Introduction

Studies of the body lengths of rattlesnakes suggest many interesting problems of growth. For example, what is the average size of a species; what is the length at birth, at maturity, and what is the maximum reached? How much variation is there in a brood, or a less homogeneous group? How much difference is there between subspecies, or between varieties which are not sufficiently divergent to warrant subspecific recognition? Are there differences between the sexes? Is there a generically consistent ratio between the smallest and largest individuals of the same species? These and related questions may be investigated, and such answers secured as the material at hand permits. But the data used must be based on authentic measurements; in no phase of rattlesnake life have there been more wild tales and exaggerations than in connection with length.

There are three episodes in the life of a snake at which, if average lengths can be determined, interspecies comparisons may be made. These are, length at birth, length on reaching the reproductive stage, and ultimate length. Of these, the length at birth is the most definite. From broods we may secure minimums and averages, particularly if we are sure that the measurements were made immediately after birth. Here the condition of the rattle will give some indication of the age of the specimen; if the prebutton be present the snake is but a few days old, for the prebutton is lost with the first shedding. But we must be sure that the mother has not been too long in captivity, since there is evidence that the young are affected by unnatural conditions, and we must avoid freaks which will distort the statistics. When juveniles are found in the wild, the date of collection will be of interest, as the age may roughly be determined from the normal time for the birth of young in that area.

The length on entering the reproductive stage can be determined from the minimum lengths of females containing developing eggs. Data thereon are not easy to secure; also it must be remembered that the females carry eggs for almost a year before the birth of their broods, and these young mothers grow during gestation.

As to the ultimate lengths, we must choose between what might be termed average large adults in any species, and record-breaking individuals. One who has handled many snakes notices that unusually large specimens are occasionally seen in every species--adults so large, compared with the ordinary run of the species, as to excite comment. Whether these giants are very old, or are merely freaks which have grown to large size through exceptional physiological or ecological conditions, is an interesting problem.

Size is a matter of interest to the general public; almost the first inquiry made with respect to any species of snake concerns the length which it attains. Likewise, in the case of the rattlesnakes, size is of some practical importance in its bearing on the hazard of snake-bite, for the larger snakes are the more dangerous. This is because of their greater quantity of venom and deeper-penetrating fangs; the longer reach which they can attain in a strike; the increased weight and drive behind the strike (tending to force the fangs through interfering clothing); and the fact that they are likely to strike somewhat higher, possibly above boots, puttees, or other leg protection.

Within a species which inhabits large areas, or areas of widely divergent ecological conditions, there will be found size differences which may be insufficient in degree or consistency to justify subspecific designation (unless accompanied by modifications in other characters), but which nevertheless complicate generalizations with respect to size. Amongst the rattlesnakes this situation frequently occurs. Thus in the widely ranging Crotalus viridis viridis,* the prairie rattlesnake, we find a progressive decline in size from Montana southward through Wyoming and Colorado to New Mexico, and thence westward into Arizona, where the differentiation is sufficient to warrant recognition of the stunted subspecies Crotalus viridis nuntius. In C.v. oreganus, the reverse is the case, the southern California specimens growing to a larger size than those in Washington. In scutulatus the southern Arizona desert specimens are larger than those found in the mountains about Prescott. The largest specimens of cinereous seem to be found in southern Texas; nowhere else in the extensive range of this species are the huge six footers so frequent, if indeed they occur at all. And thus it is with all wide-spread species--statements of average length can be only approximations unless territorially defined.

Conditions Affecting Accuracy of Data

Generalizations concerning the lengths of adult snakes must be made with caution when preserved collections constitute the basis of an investigation. Of the smaller and rarer species it is usually the practice to collect and preserve every available individual, and therefore museum collections are likely to be fairly representative of populations in the wild. But of the larger species it must be recognized that in collecting there is often a conscious discrimination in favor of the smaller specimens; the large snakes are so bulky and involve such difficulties in the field (in their requirement of large containers and supplies of liquid) that they are rarely preserved. Thus, a collection of Crotalus cinereous will seldom reveal the average adult or the ultimate size to which this species grows in any area. Often where material is accumulated jointly for

* This species was referred to as Crotalus confluentus in the first three articles in this series (Occ. Papers S.D.Soc.Nat.Hist., No.1, Aug.10, 1936). Another important change has been the substitution of Crotalus cinereous for Crotalus atrox as the name of the western diamond rattlesnake. The reasons for these alterations in names will be found in Trans.S.D.Soc.Nat.Hist., Vol.8, No.20, p.194, 1936.

natural history and zoological collections, there is a definite selection between the sizes, the larger being sent alive to the zoo while the smaller individuals are preserved for study in the museum.

In some areas long persecution may noticeably diminish the average size of the adults of a species. Old settlers in certain districts state that rattlesnakes do not grow to so large a size as they once did; and this may not always be an exaggeration, since destruction may limit the size reached. An example outside the rattlesnake field is the size of the alligators in many areas in Florida and Louisiana; here it seems to be admitted that hunting this animal for its hide has prevented its reaching the sizes once attained.

In gathering data on length, measurements made immediately after a specimen has been killed, but before it has become hardened in preservative, are more accurate than live measurements or those made of specimens fully set; for under such circumstances the muscles are completely relaxed; the specimen can be laid along a rule and the length obtained undistorted by curvature.

The measurement of live specimens involves some difficulty, particularly with large individuals. It will usually take two persons to control a snake, for it must be stretched and held for several moments until the muscles become tired and relaxation takes place, so that an accurate measurement can be made. With some experience live specimens can be measured with an individual accuracy of about 3 per cent and a cumulative accuracy within one per cent, as checked by groups measured first alive and then dead.

When measurements are made of preserved specimens allowance can be made for shrinkage. A measurement of 30 specimens of C.v. viridis before and after setting in alcohol, indicated an average shrinkage of 1.9 per cent. Fourteen specimens of C. cinereous showed a shrinkage of 1.5 per cent. Where the preserving process dries and hardens the material more than alcohol, greater discrepancies are to be expected. If possible a coiled specimen should be stretched, a section at a time, if necessary, along the rule; rolling is inaccurate. Specimens which are much hardened and contorted in preservation can be measured with fair accuracy by the careful application of a flexible wire down the mid-dorsal line.

Dimensional data from skins are of little value, most of the great exaggerations of length being based on stretched skins. It is well known that up to 50 per cent may have been added to the true length of a snake when the remains are preserved in the form of a dried, stretched skin. No skin measurements have been used in the determinations which follow.

Having pointed out some of the difficulties and inaccuracies involved in a study of length, we now proceed to an investigation of the statistics of about 8000 rattlers, many of which were measured just after the snakes had been killed.

The Curve of Growth--General

The growth-curve of the rattlesnake cannot be determined by observation of caged specimens, for our studies show that the entire life cycle is seriously distorted by captivity. Most rattlers do badly in captivity; they are a prey to self-imposed starvation and to disease; and even when they apparently thrive, as some do, rattle studies indicate that they do not follow the normal growth-trend of the wild. The artificial temperature and food conditions of the reptile house affect the growth.

Thus if we are to determine the normal growth-curve we must obtain our data by considering a large number of specimens as collected in the field, securing from each snake a single point on the curve. Also our material, for each species or subspecies, must be so chosen as to be undistorted by variable environments; necessarily the specimens must be territorially restricted. We must treat the sexes separately, as we have reason to believe that there is a sexual differentiation, the magnitude of which it will be desirable to ascertain.

Because of individual and family variations, the curve of growth of a species, however restricted territorially, will be a surface generated by the translation of some changing dispersion curve. This curve may approximate the probability curve, or normal curve of error. From a large number of specimens well distributed in age we can get an approximation of the average growth trend; this is the backbone of our surface. From other large series, captured at the same time and place, we can secure a cross section of the dispersion surface and thus determine the form of the generating curve. The latter determination may be complicated by the overlapping of successive life-classes; for it is evident that as the adult state is reached, and growth declines, the dispersion of individual variations may prevent the accurate segregation of the snakes differing in age by only a year. In other words the backbones of our hypothetical figures representing successive year-groups will draw nearer together, while the dispersions represented by the cross sections flatten and spread.

The most accurate results would be attained if we could secure large series of specimens at relatively short intervals throughout the year. This is impossible amongst the rattlesnakes, for such large series can be caught only at two seasons--when the snakes are entering and dispersing from hibernation. At other times they are so well scattered and hidden that few can be found. Thus, Mr. C.B. Perkins, within three years in raids on dens in prairie-dog towns near Platteville, Colorado, collected over 800 prairie rattlesnakes at the beginning and end of the hibernating season; but during the summer, in the same and contiguous areas, assiduous collecting produced less than half a dozen specimens.

In our studies we must be assured that the series considered have not been collected by some method that has been selective--we must have "run-of-mine" material. This precaution is especially necessary in the concentrated collections; the chronologically continuous series will usually be of random type, although sometimes discriminating against the largest specimens, as previously mentioned. We must

Table 5

STATISTICS OF RATTLESNAKE BROODS

Species or Subspecies	State	Foot Note*	Number in Brood	L e n g t h			Standard Deviation mm.	Coeff. of Variation Per Cent
				Min. mm.	Max. mm.	Ave. mm.		
<i>C.basiliscus</i>	?	1	13	285	314	299.9	7.38	2.46
"	Sin.	5	24	310	329	321.7	5.51	1.71
<i>C.m.molossus</i>	Ariz.	2	4	235	274	251.7	16.47	6.56
<i>C.cinereous</i>	"	2	8	231	243	238.5	4.18	1.75
<i>C.ruber</i>	Calif.	2	9	299	316	307.2	6.19	2.01
<i>C.scutulatus</i>	Ariz.	3	9	224	243	231.3	5.60	2.42
"	"	1	6	148	194	164.7	14.75	8.97
<i>C.v.viridis</i>	N.M.	3	8	239	273	261.1	11.56	4.42
"	"	4	10	276	325	297.7	14.40	4.83
"	"	3	14	248	290	261.8	10.84	4.14
"	"	4	15	233	276	263.4	7.84	2.97
"	"	4	17	222	277	259.9	14.25	5.53
"	"	4	11	240	263	252.5	6.55	2.59
"	Mont.	3	20	236	281	259.8	11.66	4.50
"	"	3	11	232	281	255.7	14.75	5.76
"	"	3	13	238	270	253.2	7.93	3.13
"	"	3	9	214	267	243.3	17.00	6.99
"	"	3	6	176	268	248.8	33.91	13.64
"	"	3	7	226	257	244.7	10.85	4.43
"	"	5	19	204	272	253.2	19.36	7.64
<i>C.v.nuntius</i>	Ariz.	2	7	135	146	139.7	3.73	2.66
<i>C.v.oreganus</i>	Calif.	2	7	256	267	260.9	3.83	1.46
"	"	4	7	260	286	273.6	8.27	3.02
"	"	3	12	225	243	230.7	5.40	2.34
"	"	1	10	231	260	242.4	7.96	3.28
"	"	4	13	265	283	273.3	6.73	2.47
"	"	3	5	295	305	298.6	3.44	1.15
<i>C.h.horridus</i>	?	4	8	275	295	282.9	5.77	2.03
<i>C.l.klauberi</i>	Ariz.	1	4	136	142	139.7	2.28	1.63
<i>S.c.catenatus</i>	Mich.	4	8	223	235	230.1	4.00	1.73
"	Wis.	6	6	171	195	184.7	9.28	5.02

- * 1. Born dead.
 2. Killed before birth.
 3. Killed or measured within a few days after birth.

4. Measured from a week to two months after birth.
 5. Possibly more than one brood.
 6. History uncertain

also be sure that the dates represent dates of preservation, with no intervening periods of captivity, between collection and preservation, of sufficient duration to distort the result by aberrant growth.

Coefficient of Variation at Birth

We may well begin our investigation with a study of broods. Such groups should contain variations which are solely individual or sexual in character; taken as units they should naturally eliminate parental, racial, or environmental variables.

In Table 5 there are set forth certain statistics on 31 broods of rattlesnakes totalling 320 individuals. Attention should at once be directed to the fact that these by no means constitute an ideal set of data. For truly accurate studies of this kind we should have available a large number of broods, measured immediately after birth and born to mothers which have been in captivity only a few days. Under such circumstances we would have conditions closely approaching nature. As it is, we find that some of these broods were born dead; others were removed from dead mothers; and still others were not measured until a considerable time after birth. The mothers had been in captivity for unstated periods. Thus these broods are not presented as indicating normal species lengths at birth, although a few do so fairly enough. Not only are the averages subject to question but the minima and maxima are even more doubtful. Some are freaks which would not long survive; and in any case such extreme specimens are likely to give an inaccurate picture of group dispersion.

But the coefficient of variation,* as shown in the last column in Table 5, is of decided interest and is little affected by the conditions which detract from the value of the absolute measurements. For instance, this coefficient will not be much affected by the date of measurement, whether before or after natural birth, provided the brood was not allowed to survive so long that differential growth began. We find that there are few instances, wherein the coefficient of variation exceeds 5 per cent, which cannot be explained by one of two conditions: either there was too long an interval between birth and measurement; or the brood is a small one and the high coefficient is produced by one or two aberrant individuals. If we take only broods of 8 or more individuals and omit those measured more than a week after birth, we have an average coefficient of variation (not weighted) of 3.5 per cent.

Another analysis of the same data is made thus: We first determine separately the mean length of each brood, following which each specimen is given a rating in per cent of the mean of his brood. Another way of putting this is to say that the average of each brood is considered to be a snake 100 mm. long and the hypothetical length in mm. of each individual of the brood is determined by the ratio of its true length to the mean of that brood. Thus the lengths are reduced to a comparable basis and may be assembled in a

* The mean divided by the standard deviation expressed as a percentage.

single statistical array. By this method we determine that the composite coefficient of variation of these 31 broods of 320 young rattlesnakes is 4.5 per cent. With this combined array we are at once impressed with the presence of certain aberrant specimens, particularly stunted individuals, which affect the result out of all proportion to their number. If we eliminate the four most outstanding (and undoubtedly defective) little snakes, the remaining 316 have a coefficient of variation of 3.8 per cent. If we go still further and drop out the 9 smallest and 2 largest specimens the coefficient is reduced to 3.3 per cent.

Based on all of these data I think it safe to conclude that the coefficient of variation of most natural broods will run below 4 per cent.

The coefficient of variation, while frequently applied in statistical work as a measure of dispersion (it is often called the coefficient of dispersion), is not especially easy to visualize. In the present instance the following figures will serve to amplify the statement of dispersion implied in this coefficient. I have assumed that the dispersion follows the normal curve of error, which is later shown to be approximately the case.

Coefficient of variation in per cent	Limiting range of half the spec- imens in per cent of the average	Limiting range of nine-tenths of the specimens in per cent of the average
4	97.3 to 102.7	93.4 to 106.6
3.5	97.6 to 102.4	94.2 to 105.8
3	98.0 to 102.0	95.1 to 104.9
2.5	98.3 to 101.7	95.9 to 104.1
2	98.6 to 101.4	96.7 to 103.3

To interpret these figures further let us assume that 4 per cent is a safe figure to use, as seems to be indicated by the data previously developed. Then in a brood (of C. ruber, let us say) averaging 300 mm. in length, half the specimens will fall between 292 and 308 mm., while 90 per cent will probably be no shorter than 280 mm., nor longer than 320. This gives a more complete picture of likely variations than a statement of minimum, average, and maximum, since the latter statement affords no idea of how closely the individuals cluster about the mean, and depends too much on freak specimens. Thus we note a rather impressive constancy of size in broods of young rattlers.

I have previously shown* that there is a positive correlation between the size of a female rattlesnake and the number of her brood. It has been suggested by Mr. R.M. Perkins, of the St. Louis Zoo, that smaller broods average larger in individual size. This is a correlation which might well be investigated, but at present there are not available a sufficiently large number of broods from the same species and locality, measured under uniform conditions, to prove the point. The few Montana broods of viridis indicate a positive correlation between the size of a brood and the average size of the young comprising it, which is contrary to the opinion expressed by Perkins. But admittedly

* Occ.Pap.S.D.Soc.Nat.Hist.,No.1,p.16

the data are too few to be conclusive. This part of the problem must await the availability of adequate material.

The correlation, if any, between the size of the mother and the size of the offspring would likewise be an interesting problem. Possibly external factors, such as food availability during gestation, would tend to mask the results.

In Table 5 we observe a difference in the average lengths of broods from a single locality, even though measured immediately after birth. This is parental or genetic variation, as opposed to racial or territorial variation, such as would be found between broods from different areas. A study of the variation in such averages must also await more material. But a closely allied investigation can be made by comparing the coefficients of variation of broods with those of miscellaneous, but territorially homogeneous, groups of young. Of this type we have available data on four lots totalling 602 young snakes. These are as follows:

(1) A collection of 82 Crotalus molossus nigrescens from La Colorada, Zacatecas, secured by Messrs. Hobart M. Smith and David H. Dunkle. Some of these were born alive and were preserved within a day or so after birth, the prebuttons being still present; the rest were nearly ready for birth.

(2) The San Patricio collection of 139 Crotalus cinereous. These were born to several mothers collected in the vicinity of San Patricio, Texas, and were sent to me alive by Hiram J. Yoder. They were born about August 15 to 20, and were measured September 29 to October 2.

(3) The Pierre, S.D., collection of 152 young Crotalus viridis viridis sent to me through the courtesy of A.M. Jackley and Dr. H.K. Gloyd. They were collected at dens in October and were preserved in late December, or early February. They received water but no food while in captivity.

(4) The Platteville, Colo., collection of 229 juvenile C.v. viridis, sent me by C.B. Perkins. Most of them were collected in raids on dens in early October and were preserved about a month later. A few were collected at the dens in spring (mid-April) and were preserved in early May.

The raw data of these broods are presented in Table 6, and the calculated statistics in Table 7. Of particular interest is the coefficient of variation. This shows an increase (compared with the figure of 3.5 per cent averaged by the separate broods) to 5 for the groups of broods, and to 8 or $8\frac{1}{2}$ for the collections resulting from den raids. The first increase of $1\frac{1}{2}$ per cent may be considered attributable to parental heterogeneity, which in turn may be either genetic, environmental, or both. The additional increase from 5 to $8\frac{1}{2}$ results, I believe, from the differential growth between birth and preservation. Certainly we may expect that differences of inheritance and of luck in securing food, will become increasingly manifest as the young snakes roam abroad prior to hibernation. It must also be remembered that they are not all of exactly the same age; probably as much as a month may elapse in any

Table 6
LENGTHS OF YOUNG RATTLESNAKES

Number of Specimens in each Length-Class
(Segregated by Sexes)

Length- Class	Zacatecas nigrescens			San Patricio cinereous			Pierre viridis			Platteville viridis		
mm.	M	F	Total	M	F	Total	M	F	Total	M	F	Total
240-9										1	1	2
250-9	2	5	7					1	1		2	2
260-9	8	7	15							9	13	22
270-9	14	4	18	2	4	6	2	1	3	20	16	36
280-9	4	12	16	7	6	13	3		3	10	27	37
290-9	10	9	19	9	13	22	4	2	6	18	12	30
300-9	5	1	6	18	13	31	4	5	9	11	16	27
310-9	1		1	25	15	40	4	11	15	15	10	25
320-9				10	5	15	10	16	26	18	3	21
330-9				5	4	9	8	7	15	8	2	10
340-9				1	2	3	16	7	23	8	2	10
350-9							10	11	21	2	1	3
360-9							8	6	14	2		2
370-9							7	4	11	1		1
380-9							3		3			
390-9							1	1	2		1	1
Total	44	38	82	77	62	139	80	72	152	123	106	229

Table 7
STATISTICS OF YOUNG RATTLESNAKES

	Zacatecas nigrescens	San Patricio cinereous	Pierre viridis	Platteville viridis
Number of specimens	82	139	152	229
Average length, mm.	280.2	307.6	335.7	298.3
Standard deviation, mm.	14.7	15.7	26.4	25.8
Coefficient of variation, %	5.26	5.12	7.88	8.65
Maximum range, mm.	250 to 318	274 to 344	255 to 394	246 to 394
Interquartile range, mm.	270.3 to 290.1	297.0 to 318.2	317.9 to 353.5	287.6 to 309.0
Probable error of the mean, mm.	1.09	0.90	1.44	1.15
Average length, males, mm.	281.5	309.0	339.0	304.2
Average length, females, mm.	278.7	305.8	333.7	291.5
Standard deviation, males, mm.	15.0	14.6	27.6	26.7
Standard deviation, females, mm.	14.2	16.8	24.7	22.9
Significance of difference between males and females*	0.87	1.18	1.25	3.88

* Expressed in terms of the
standard, not probable,
error of the difference

area between the birth of the first and last broods. On the other hand there will be one contrary factor tending to curtail dispersion, namely the elimination of the defective specimens which do not long survive but which were included in the broods.

Shape of Dispersion Curve at Birth

The extent of the dispersion in length of young rattlesnakes having been determined, we proceed to an investigation of the nature of the dispersion curve. The chi-square test* for closeness of fit to the normal probability curve was applied with the following results:

<u>Group</u>	<u>P</u>
Zacatecas <u>nigrescens</u>	0.51
San Patricio <u>cinereous</u>	0.64
Pierre <u>viridis</u>	0.77
Platteville <u>viridis</u>	0.01
Composite broods	0.25

This tabular statement means that, in the cinereous case for instance, if we had other random selections from the same population to test and the dispersion were in fact normal, the closeness of fit to the normal curve of these new samples would be no better or would be worse than was found in our particular sample, in 64 cases out of 100. Thus the odds are strongly in favor of the distribution being really normal. Even in the case of the composite broods the odds of 1 out of 4 in favor of normality are by no means excessive, although some of the assumptions made in securing composite results render this less conclusive than the first three groups.

It is only in the case of the Platteville series that we find no evidence to suggest a normal distribution. Here (see Table 6) the mode is smaller than the mean; the rise to a maximum frequency is abrupt in the smaller sizes with a gradual falling off toward the larger. The cause of this divergence from a normal distribution is not known; it may result from the specimens having been kept so long in captivity prior to measurement, thus permitting differential growth. It is not the result of the beginning of sexual dimorphism. It is true that the females taken alone show a value for P of 0.049, which is a distinctly closer approach to a normal distribution than the composite curve of both sexes. But the male value of P is 0.0018; in this curve there is a sharp early peak with a gradual slope toward the larger sizes. However, we do not believe that this single group, kept for a rather long time in captivity, and partially the result of autumn and partly of spring collec-

* For a discussion of the chi-square test for closeness of fit see such statistical texts as Fisher, Statistical Methods for Research Workers, Fourth Edition, 1932, p. 80; Mills, Statistical Methods, 1924, p.543; Pearl, Introduction to Medical Biometry and Statistics, Second Edition, 1930, p.315; Yule, An Introduction to the Theory of Statistics, Tenth Edition, 1932, p.370; Davenport and Ekas, Statistical Methods in Biology, Medicine and Psychology, Fourth Edition, 1936, p.47.

tions, is of importance in controverting the evidence of the other groups, which indicates that the distribution of the sizes of rattlesnakes at birth closely approaches the normal curve of error.

Sexual Dimorphism at Birth

Of the 31 broods available, the males average larger in 17 and the females in 14. This is a difference slightly in favor of the males but by no means convincingly significant. A composite study of the broods, by the method of equalizing averages, shows a small male superiority.

Referring to Table 7 it will be noted that in the Platteville group of young viridis there is a significant difference in length between the males and females. In the other three groups the difference is below the level of significance.*

It will be noted that while in the case of the Zacatecas, San Patricio, and Pierre groups the average difference between the males and females is not significant the difference in each instance is in favor of the males. Cumulatively this adds weight to the difference.

By the method of determining the length of each young snake as a percentage of the mean of his group, so that several groups may be combined, we find that the combined significance between the sexes of the Zacatecas, San Patricio, and Pierre series is 1.89, which means that there are only about 6 chances in 100 that the result is due to chance and is not a real difference. The length-ratio of the average female to the average male is .98.7 per cent. I therefore conclude from all of these data that juvenile male rattlesnakes average slightly larger than females, the difference being only about one per cent.

One point remains to be mentioned: While the deviation of any individual from the mean of his brood is as likely to be above the mean as below, most extreme deviations are below. That is, stunted or dwarfed specimens occur at birth, but not giants; variants falling 10 per cent below the mean are more often encountered than those exceeding the mean by an equal amount.

* There is some non-uniformity in statistical texts as to the level of significance assumed in cases such as this. Usually the figure 3 is taken as the lower level of significance; but some statisticians base their conclusions on the difference of the means divided by the probable error of the difference, while others divide by the standard error of the difference. These are quite different levels, for a ratio of 3 using the probable error is only equivalent to a ratio of 2 using the standard error (2.0235 to be exact). Using 2 and the standard error there are 4.55 chances in 100, or 1 in 22, that the difference is the result of chance in sampling, rather than a real difference in the populations. With a ratio of 3 (again using the standard error) the chance is only 1 in 370. I will usually consider 2 as the lower level of significance on a basis of the standard error of the difference.

The Dispersion of Size Among Young of the Year

We have now completed a survey of the nature and extent of variations in length, and also of sexual dimorphism of juvenile rattlers before and during their first hibernation. Before passing to consideration of the curve of growth (the backbone of the growth surface) it will be advisable, in the interest of clarity, to continue the investigation of the same factors amongst these young rattlers during their first spring. Beyond this stage of life we cannot proceed by year-classes, for in the second year the young adults have become so variable in size, through the effects of genetic and environmental factors, that they can no longer be segregated with certainty from the three-year-olds. As we cannot be sure we have a single year-class under consideration it is impossible to determine the dispersion by age-classes.

But in the first spring when the young snakes are about 6 months old they can be quite readily segregated from the next older group aged $1\frac{1}{2}$ years (especially if the number of rattles is used as an additional check) and hence these may well be investigated.

As I have stated, our material must be distributed chronologically, yet it must be territorially homogeneous to avoid the effects of incipient racial differentiation. A series of C.v. oreganus collected in San Diego County, California, comes nearest to fulfilling the requirements, there being available 189 young of the year collected from March to June inclusive. The statistics of these young snakes, grouped by months, are presented in Table 8.

Upon these results the following comments are pertinent: Differential growth has become effective; the coefficient of variation, which averaged below 4 per cent in the broods and from 5 to $8\frac{1}{2}$ per cent in the groups of recently-born young, now ranges from 10 to 17 per cent (13 to 16 with the sexes combined) and averages 14 per cent. While the difference in length between the males and the females is still statistically below what is usually taken as the level of significance, nevertheless the males are longer in each case and the sexual differentiation is on the increase as the snakes grow older. The average difference in favor of the males is slightly over 3 per cent.

There is not a sufficient number of specimens available in any one month to determine the adherence of the dispersion to the normal probability curve. However, we find the average rate of growth of these young snakes to be 16 mm. per month. Using this figure we may calculate the hypothetical length of each snake as of May first. For the entire lot of 189 specimens, thus adjusted, we find a combined coefficient of variation of 15 per cent. The chi-square test for closeness of fit to the normal curve gives $P=0.11$ which indicates a fair chance that the true curve of this population of adolescents is normal. The curve in our particular sample is slightly flatter than the normal curve.

As a rough check on this analysis we have assumed those Platteville rattlers having complete rattle strings of from 4 to 6 segments to represent a sample of the adolescent population, about 8 months older than the oreganus group previously discussed. The coefficient of variation

Table 8

STATISTICS OF YOUNG OF THE YEAR: SAN DIEGO COUNTY C.y. oregonus

Month	March		April		May		June	
	M	F	M	F	M	F	M	F
Sex								
Number of specimens	13	13	28	27	33	29	22	24
Average length, mm.	365.3	356.8	373.1	373.0	396.3	378.0	414.0	389.5
Standard deviation, mm.	36.0	56.6	58.3	36.8	67.0	52.6	65.2	44.8
Coefficient of variation, %	9.9	15.9	15.6	9.9	16.9	13.9	15.7	11.5
Maximum range, mm.	303 to 431	277 to 505	284 to 523	312 to 442	276 to 514	270 to 517	324 to 555	313 to 487
Interquartile range, mm.	341.0 to 389.6	318.6 to 395.0	333.8 to 412.5	348.2 to 397.8	351.1 to 441.5	342.5 to 413.5	370.0 to 458.0	359.3 to 419.7
Probable error of mean, mm.	6.73	11.02	7.44	4.78	7.88	6.59	9.16	6.18
Significance of difference between males and females	0.44		.008		1.20		1.47	

of this group is found to be only 7.4 per cent compared with 15 per cent in the San Diego County oreganus. I believe the difference is partly the result of the ecologically more complex area inhabited by oreganus, the fact that the viridis specimens are more concentrated chronologically, and finally the method of selecting the viridis specimens, which eliminates some of the extreme individuals, for the rattles are not always a trustworthy age indicator.

It is my conclusion from these two sets of data that a population of young rattlers from a single area at the age of eight months (a part of which has been spent in hibernation) has a coefficient of variation of 10 to 12 per cent.

The Growth Curve

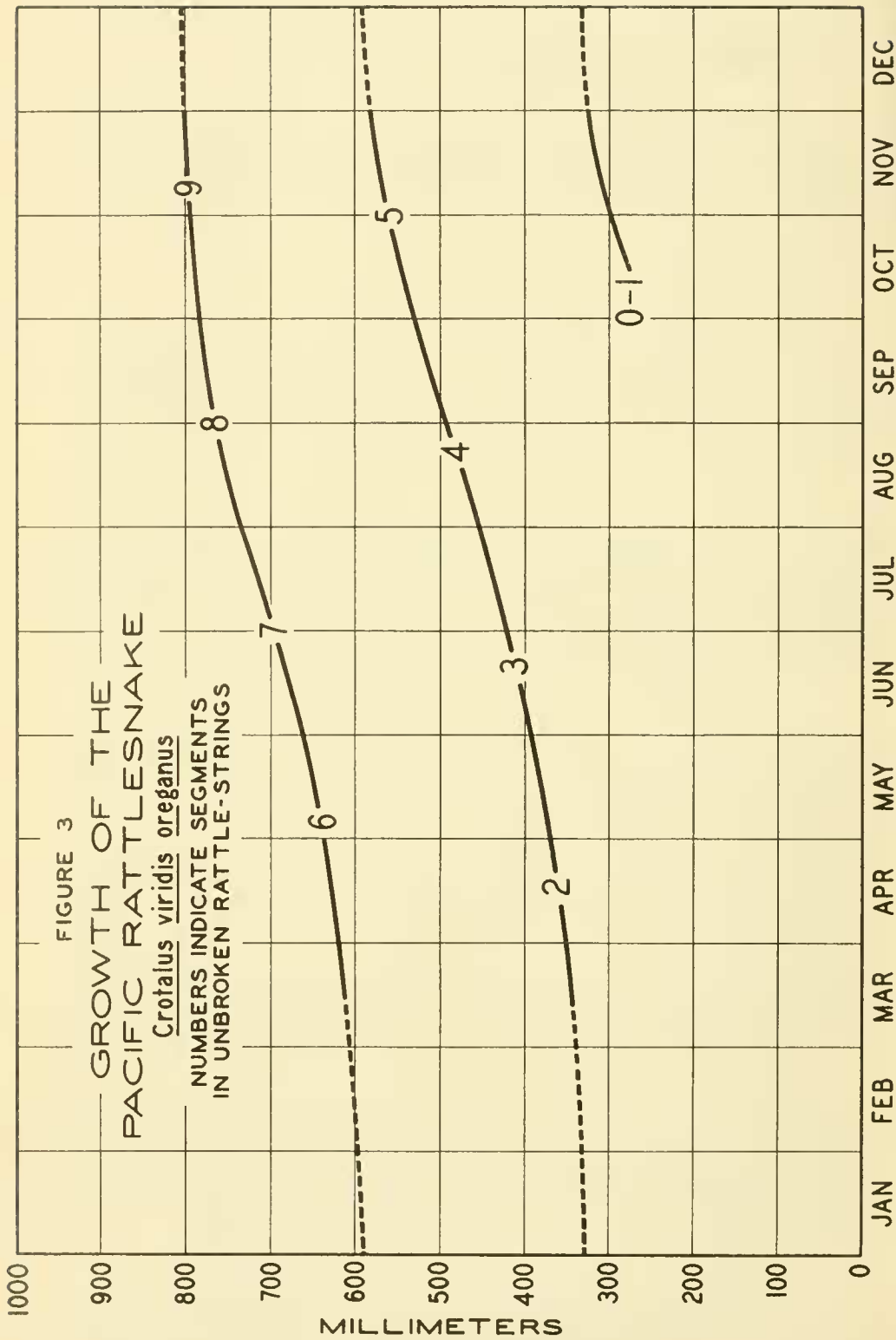
The determination of the average growth curve, the backbone of the growth surface to which reference has been made, is best surveyed by purely graphical methods. The data available from a single species of rattlesnake from a single area are found too limited to permit an analytical attack.

The San Diego County C.v. oreganus specimens again provide our best set of data, for while larger series are available from some other areas, they are not so well distributed chronologically. Of the oreganus series there are 496 specimens of all ages, with collection dates fairly well distributed throughout the year, although the spring is better represented than the other seasons.

The data of these specimens were entered upon cross-section paper, each specimen being indicated by a single point, the length in millimeters being the ordinate of that point and the date of measurement the abscissa. If the snake retained a complete set of rattles the point was designated by the number of rattles in the string; if the string was incomplete the coordinate was indicated by a cross. The sexes were distinguished by colors, and in order further to render the data representative of a homogeneous group, the mountain specimens were indicated by a separate color. Thus we have some 500 points upon our chart, many of which are numbered. At once it is found that these points are not entirely uncoordinated in their distribution; on the contrary they cluster in zones.

In particular it is noted that trends are moderately definite during the first ten months of the life of the snake. Subsequent thereto, partly because rattlers of the particular age-class under consideration are less often captured, and partly because of the increasing dispersion in size previously discussed, there is difficulty in tracing the trend.

It may be observed that size variations in any group are related to the variations in habitat conditions in the territory occupied by that group. In other words, there is an increasing coefficient of variation of the dimensions at any single age as we spread outward, first from a single family of rattlers to a group inhabiting a restricted territory, and thence further to a population inhabiting a larger area, especially if that wider territory



contains a considerable variation in habitat conditions. San Diego County is an area of ecological complexity, but as oreganus is not found in the desert and is rare in the desert foothills, the full effect of habitat variation is not demonstrated in the subspecies here investigated. However, there are a number of mountain specimens available and these, having a considerably shorter active season, are born somewhat later and mature more slowly than those from the valleys and foothills. It should not, however, be assumed that a shorter growing season necessarily means a smaller ultimate size. There are other factors, obscure or indeterminate, which have counterbalancing influences. Thus it cannot be length of seasonal activity which causes C.v. viridis to grow larger in Montana than eastern Colorado, or C. mitchellii pyrrhus in southern California to exceed the subspecies C.m. mitchellii in southern Baja California; based on this factor alone a contrary result would be expected.

On the whole, the study of the average curve of growth--the backbone of the growth surface--has not produced the certainty of result, even for the first year of life, which I had been led to expect from a casual observation of many specimens; for analysis has not shown the close adherence to size classes that was once thought to exist. Starting with a group coefficient of variation of 5 per cent at birth (which does indicate a high degree of consistency), it has been shown that this increases to 10 to 12 per cent by the following spring. Beyond this a further dispersion is indicated. Also there may be off-season births which would further confuse the record, for there are certainly off-season matings.* The result is that the curve is difficult to fix with accuracy.

Fig. 3 represents a simplified and generalized curve of growth of C.v. oreganus, the Pacific rattlesnake, in southern California. It was prepared in part from the chart of 500 San Diego County specimens previously mentioned, reinforced by more fragmentary data from other areas. Certain conclusions on questionable points have been verified from the chronologically concentrated groups of other subspecies resulting from the den raids, particularly the Platteville and Pierre series of C.v. viridis.

Summarizing the life history of oreganus, we find that the young rattlesnakes are born between the middle of September and the 20th of October, most of them in this territory during the first few days of October. At birth they average about 275 mm. in length, the variation being from 255 to 330 mm.

Within a few hours, or, at most, a few days after birth, the initial rattle, which we have called the prebutton, is shed with the first skin-shedding, leaving exposed the first permanent rattle (the button) which is retained until such time as the string may be broken.

These young rattlers go into hibernation toward the end of November, the time no doubt depending upon the

* Our nearctic species normally mate in the spring but Wood, Copeia 1933, p.85 and Taylor, Copeia 1935, p.154 report summer matings.

climatic conditions during their first year of life. In this area, at least in the lower altitudes, they evidently do not den together in large aggregations, nor do they have fixed dates of going into and coming out of hibernation, such as characterize the activities of rattlesnakes in colder climates. On the contrary they seek seclusion more or less individually in holes and rock crevices, and are likely to issue temporarily from hibernation whenever the winter weather is propitious. At the time the young rattlers go into hibernation in their first winter, they average about 320 mm. in length, and in some instances, probably influenced by their success in obtaining food, a few have changed their skins again and have thus acquired their second rattles. The average growth between birth and initial hibernation is 45 mm., or about 16 per cent.

In the spring, although an occasional stray is captured as early as January or February, most of them are not regularly abroad until about the tenth of March. From then until the middle of June they are extremely active and at this time the juveniles, searching about for food, are captured in the greatest numbers.

Studies of the Platteville series indicate that there is a considerable loss of weight during the hibernating season, but practically no increase in length. In San Diego County, the Pacific rattlesnake, under less arduous winter conditions, shows a slight average increase in length during the hibernating season, so that by the time the young rattlers have come out in mid-March, they have reached an average length of 340 mm. A few exceed 400 mm. From this time until the end of June the growth seems to be quite constant and is rapid.

By mid-April many of the specimens have attained their second rattles and a few their third, although those which still have a single rattle are by no means absent. At this time the average length approximates 370 mm. By the end of May they have grown to 400 mm.; two rattles have become the mode, and there are more with three than with one. By the first of July the young snakes have reached an average length of 420 mm., and most of them have three rattles. In July and August, and until the end of the year, there is a distinct falling off in the number caught, since the snakes have largely become nocturnal, and we cannot draw our conclusions with the same certainty. There are indications, however, that upon the first anniversary of their births the snakes have reached an average length of 530 mm., and most of them have four or five rattles, this being their status in late September. Thus during their first year of life these rattlers have nearly doubled in length; and as their weight curve has been calculated to be $W = 550L^{3.3}$, where W is the weight in grams and L the length in meters, we find that the bulk has increased nine fold. The skin has been changed 3 or 4 times in addition to the birth-change.

Shortly after this time the adolescent snakes go into their second hibernation. Following their issuance from this hibernation in March, we trace their course with difficulty, although somewhat aided by analogy with other species which have likewise been investigated. By the first of May, most of them have six rattles, and the length closely approximates 630 mm. By July seven rattles have become

the mode, and at the time they pass their second birthday most of them have reached a length of 800 mm., and, were their rattle strings complete, would have about nine segments.

Sexual dimorphism in size is now considerable, for it begins to be quite evident at the 7th rattle. The snakes have now reached young maturity, and thereafter the growth is much slower; and, as the rattle strings are rarely complete, the acquisition of additional rattles is mere guess work, although presumed to continue at the rate of 3 or 4 per year. However there is evidence that skin changes are somewhat less frequent when body growth has become less rapid. The first mating takes place in the following spring when they are $2\frac{1}{2}$ years old, and the females bear their first young when three years old. The maximum length reached by this subspecies is about 1370 mm. (54 in.) although most adults are considerably shorter. The majority of adult males run from about 950 to 1150 mm. ($37\frac{1}{2}$ to 45 in.) and the females from 830 to 1000 mm. ($32\frac{1}{2}$ to $39\frac{1}{2}$ in.)

Similar investigations made on ruber and luca-sensis check our determination of the life cycle of ore-ganus, when allowance is made for the somewhat larger size of the first two species. Juveniles of ruber are relatively difficult to obtain for some obscure reason. But adolescents are common and frequently have complete rattle strings. Some mile-posts in the lifecycle of ruber are as follows: they are born about September 20th with an average length of 300 mm.; mid-April, length 480 mm., 2 rattles; mid-July, length 610 mm., 4 rattles; in mid-summer one year later 850 mm., 7 rattles.

Size Distribution in a Population of Rattlesnakes

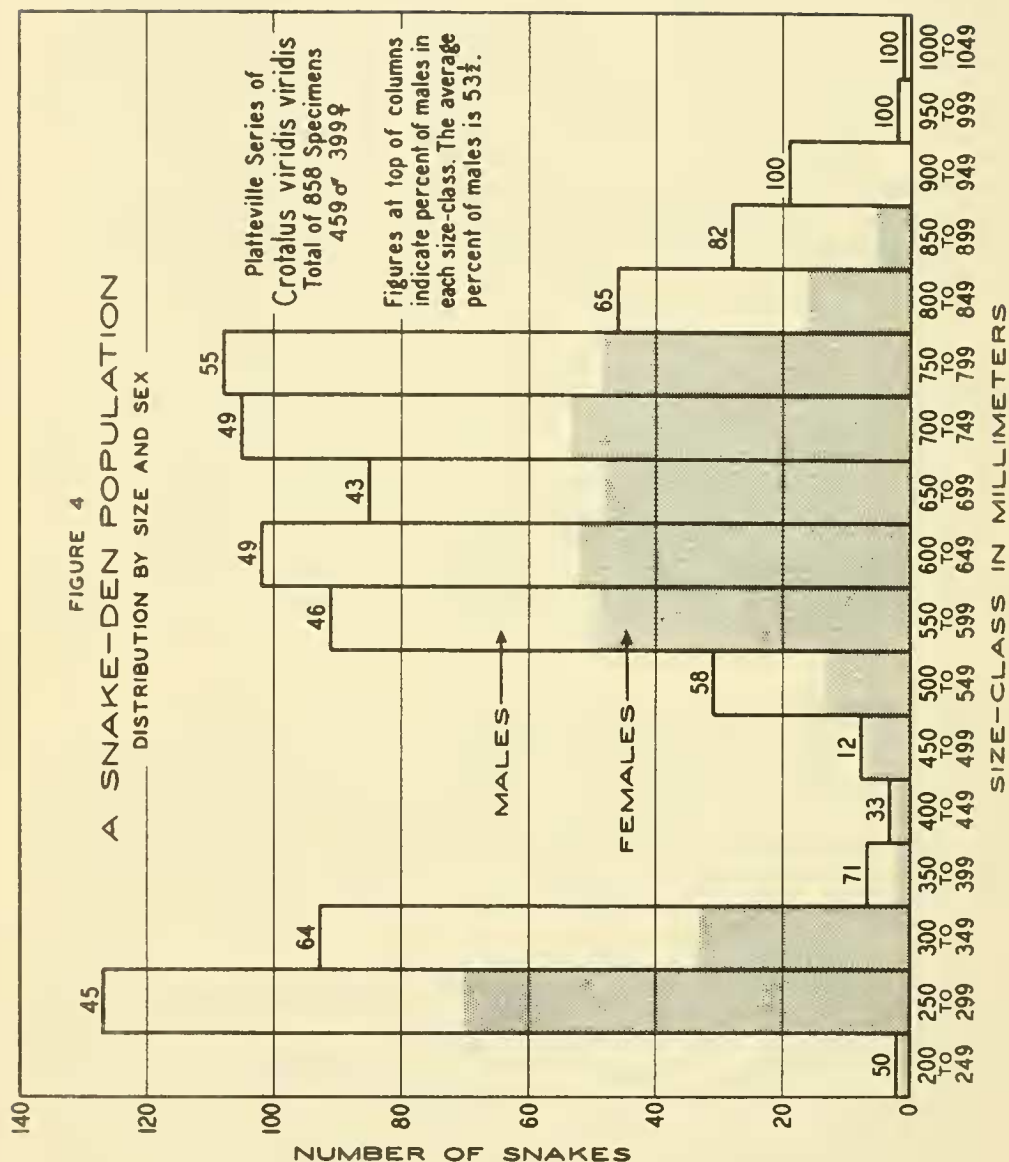
The Platteville series of 858* C.v. viridis affords the most trustworthy view which we have of a cross section of a rattlesnake population at a specific time. The circumstances surrounding the collection of this material by C.B. Perkins are well known; there was no conscious discrimination in the sizes of snakes collected.

Fig. 4 presents a histogram of the size distribution in this population, which is representative of this subspecies as it exists in northeastern Colorado at the time of hibernation. The summary is by 50 mm. increments; it was found that dividing into smaller groups tended to cause fluctuations obscuring the distribution.

We note first the quite definite division, already mentioned, between the juveniles and the next older class. In fact there are only 4 specimens falling between 380 and 460 mm.; hence we may arbitrarily set 400 mm. as the limit of the juveniles and the allocation of only 1 or 2 specimens out of 858 will be subject to question. But the segregation of the adolescents from the adults is much more difficult because of the increased dispersion in length already demonstrated, and the decreasing rate of growth. We may assume that the dip at 650-699 mm. constitutes the remnant of the division which a year before was evident at

* Excluding 3 summer specimens.

FIGURE 4
A SNAKE-DEN POPULATION
DISTRIBUTION BY SIZE AND SEX



400 mm.; but it is almost obliterated because the larger yearlings have overhauled the lagging two-year-olds, and we can no longer allocate the specimens in this range with accuracy. Were the dip more pronounced, and the overlap smaller in proportion of total specimens, it would be possible to make a tentative segregation by assuming both groups to follow an approximately normal distribution, and thus calculate the tails of the intersecting curves. Under the circumstances, however, the overlap is too broad to justify any conclusions which might be drawn from such a calculation.

Sexual Dimorphism in the Adult Stage

The proportionate distribution of the sexes indicated in Fig. 4, is of interest, especially as showing the deviations in the several size groups from the average sex ratio of $53\frac{1}{2}$ per cent males.

It is to be noted that even amongst the juveniles the males are beginning to outstrip the females in size; above 800 mm. the male predominance is strongly in evidence. The largest male is 1015 mm., the largest female only 863 mm. If we take the entire population above 400 mm., thus including both adolescents and adults, we find the males to average 712.0 ± 4.17 mm., and the females 674.1 ± 3.64 mm. The difference is 37.9 ∓ 8.2 ,* or nearly five times its standard error; thus, among the adults (even when diluted by the adolescents) there is a highly significant difference in length between the sexes. The coefficients of variation of this group are as follows: males 15.9 per cent; females 13.7 per cent; sexes combined, 15.2 per cent. These figures are important as indicating the dispersion in the subadult and adult population of a territorially homogeneous group.

If we were able to segregate the adults from the adolescents, they would, by themselves, show a greater sexual dimorphism, with a difference between the sexes approaching ten per cent. Thus, if we make an arbitrary division at 600 mm. (instead of at 400 mm., as in the previous calculation) which tends to drop out most of the adolescents and possibly a few stunted adults as well, we find that the length ratio of the females to the males falls to 0.915. This is probably close to the true adult length ratio in this subspecies.

It may seem that I have neglected an obvious line of investigation by failing to check the specimens with complete strings of 5 rattles, for most of these are no doubt adolescents, and from these we ought to be able to determine the sex-length ratio for an adolescent population. As a matter of fact this was done, but at once evidence came to light that some of the 5-rattle snakes were two year old adults, rather than adolescents, 12.6 per cent of the females being gravid. There are indications that, during the period of a snake's life when growth is rapid, i.e. the juvenile and adolescent stages, skin changes are in part a

* I use the sign \pm with the probable error, and \mp with the standard error, following the method of Davenport and Ekas, op. cit., p. 36.

function of size rather than being dependent exclusively on time or age. In other words a snake changes his skin when it is outgrown rather than at fixed periods. This nullifies any attempt to segregate adolescents exclusively by the rattle segments.

As a verification of these conclusions with respect to sexual dimorphism we may investigate a series of C. lucasensis collected in the vicinity of Cape San Lucas, Lower California, by Capt. Fred Lewis. In this series there was no conscious selection of sizes and therefore no unconscious discrimination between sexes. Also, the collection was made in the early spring, before the females become less accessible.* Our studies of the growth curve of lucasensis indicate that this snake goes into its second hibernation with an approximate length of 650 mm. To avoid including any extra large adolescents we assume a dividing line between adults and adolescents at 700 mm., the few specimens falling between 650 and 750 mm. indicating this to be a natural division point. Above this we find we have the following distribution:

<u>Length Class</u> <u>in mm.</u>	<u>Males</u>	<u>Females</u>
700 - 749		2
750 - 799	3	7
800 - 849	4	8
850 - 899	14	23
900 - 949	12	28
950 - 999	10	27
1000 - 1049	25	11
1050 - 1099	26	3
1100 - 1149	33	1
1150 - 1199	16	
1200 - 1249	11	
1250 - 1299	<u>3</u>	<u> </u>
Total -	162	110

The difference in distribution is visually evident. The average lengths are: males, 1054.6 ± 5.6 ; females, 918.8 ± 5.0 . The difference is 135.8 ∓ 11.7 , which is highly significant. The length ratio of the average female to the average male is 0.87. Hence there is no question as to the superiority in size of the males in this group of adult lucasensis. The coefficients of variation of these snakes are as follows: males, 10.8 per cent; females, 8.3 per cent. Here we have a reduced dispersion in this purely adult group quite comparable to the dispersion in the groups of young. This indicates that age is not an important factor in increasing dispersion after the adult stage is reached; in other words there is no higher dispersion in a group of adults comprising several age-classes than in rapidly growing adolescents comprising a single age class. This situation may in part result from the competitive elimination of the smaller and weaker adolescents.

* For a discussion of sex ratio and the differential seasonal activity of the sexes, see Occ.Pap.No.1, of this series, p.11.

As to the shape of the curve of these two distributions the results are conflicting. The female distribution is close to normal, P being about 0.7. The male distribution, on the other hand, is flat-topped, β_2 being 2.68 and P less than 0.01. A somewhat platykurtic distribution would be expected if the adult population were made up of successive age-classes, each having an approximately normal distribution, but exceeding the next age class slightly in average length. It is my opinion that such is the case, but these data do not definitely prove it.

It is also interesting to note that the largest male (1258 mm.) is 19 per cent longer than the average male; while the longest female (1127 mm.) is 23 per cent longer than the average female. The large female is the more unusual of the two; a snake of this length would occur only once in 286 specimens on the average, assuming a normal distribution. A male to be as unusual would be 1361 mm. long.

It may be of further interest to generalize upon the probability of occurrence of large specimens in an adult population. Assuming a normal distribution and a 10 per cent coefficient of variation, 15.9 per cent of the population should be 10 per cent or more above average size; 6.7 per cent should be at least 15 per cent oversize; 2.3 out of each 100 should be at least 20 per cent oversize; 6 in a thousand 25 per cent, and 13 in ten thousand 30 per cent or more oversize. Of course these calculations are based on homogeneous populations. One cannot judge the probable distribution of very large sized cinereous in Texas based on data accumulated in Arizona. I am of the opinion that when much more extensive series are at hand than have been available to me, it will be found that exceptional specimens occur somewhat more frequently than would be expected with a normal distribution, as there is evidence that the upper "tail" of the curve of size distribution is slightly prolonged.

Continuing the sex-length ratio investigation further, we have determined the sex-length ratio in several other forms of which relatively large numbers of adults are available. We have, however, made a further restriction by taking only territorially homogeneous groups, in order to avoid possible aberration, such as would occur if there were a territorial size differentiation within a species, and a large proportion of one sex were available from one area, and a preponderant number of the other sex from another. In each instance we have made the segregation between adults, which are included in the computation, and the adolescents, which are excluded, at approximately the length of the smallest females carrying eggs. This method tends to favor whichever sex is in reality the smaller, since it will exclude more of the smallest adults of that sex, and correspondingly include more of the largest adolescents in the other. Thus, this method of computation equalizes the sexes to a slight degree, and the true sex-length ratios are lower than are here determined. The results are set forth in Table 9.

It is observed that, with the exception of cerastes, the females are smaller, the F/M ratio falling between 84.6 and 93.6 per cent, with an average of 89 per cent. There is no doubt that in most species of adult

Table 9

ADULT SEXUAL DIMORPHISM IN TERRITORIALLY RESTRICTED

SERIES OF RATTLESNAKES

Species or Subspecies	Territory	Minimum Size Included	Number of Specimens		Average Length, mm.		Ratio F/M per cent
		mm.	M	F	M	F	
C.m.molossus	Arizona	700	37	23	967	875	90.5
C.cinereous	Arizona	750	87	56	963	873	90.6
C.lucasensis	Cape San Lucas, Baja California	730	162	110	1055	919	87.1
C.scutulatus	Arizona	650	121	48	858	754	87.9
C.v.viridis	Platteville, Colo.	600	274	222	753	689	91.5
C.v.lutosus	Utah & Nevada	650	96	48	875	784	89.7
C.v.oreganus	Pateros, Wash.	550	127	83	691	599	86.7
C.m.mitchellii	Cape San Lucas, Baja California	600	49	27	842	788	93.6
C.cerastes	Colorado Desert, California	440	53	42	537	555	103.3
C.l.klauberi	SE. Arizona	380	37	32	528	447	84.6

rattlesnakes the males exceed the females in length by about ten to twelve per cent. Before investigating the peculiar deviation in cerastes it will be well to see if there are other species in which the females are of superior size.

Table 9 shows not only the average size superiority of the males, but also their superiority in numbers in these representative populations, a fact to which attention has been directed before. It is necessary to recall the reasons for the larger numbers of the males, since it would otherwise be thought that the limit in size used in selecting these groups had been set low enough to include all the adult males but not all the adult females. This is only slightly the case; as has been shown in Section II of this series, the greater number of males in collections is due partially to an actually greater number in the population to the extent of probably ten per cent, and a difference in activity (partly seasonal) which leads to more males being captured.

To continue our investigation into other species we select the larger individuals available, comparing the averages of the ten largest of each sex. Where large series are at hand, with the sexes nearly equal in numbers, or represented in approximately the same ratio as found in nature, this will give a fairly valid comparison. However, if, in our available data, either sex greatly outnumbers the other it will be unduly favored, since the larger the number of specimens the closer to the upper limit will be the ten specimens taken as representative. In such a case the representation of the overabundant sex has been reduced by first selecting at random a group of specimens equal in number to those available of the other sex, after which the ten largest of each of these equal groups are taken. Where less than ten full sized adults are available in either sex, the other has been correspondingly reduced by random selection.

The results of this investigation are presented in Table 10. While this table gives a moderately reliable index to the sex-length ratio in each species, especially when there have been available at least 10 large adults in each sex, as indicated in the first column, it should not be given particular significance beyond this point. Except in the case of the smaller species, and then only where large numbers of adults are available, the table is not satisfactory for interspecies comparisons; for, as has been pointed out, the larger species are not fairly represented in collections by large individuals; and thus the average figures are likely to be distorted downwards. In the case of three subspecies showing considerable territorial variation, C.v. viridis, C.v. oreganus, and C.v. nuntius, territorially restricted series are employed; the first two where they reach their maximum development in size, and the last in the area around Winslow, Ariz., where this subspecies shows the greatest differentiation from its parent form.

In every instance but one, where anything approaching a representative series of adults is available, the superior length of the males is again evident. Once more cerastes is conspicuous in its deviation. In this species not only do the ten largest females exceed in size

Table 10
RELATIVE SIZES OF LARGE MALES AND FEMALES

Species or Subspecies	Number of each Sex	Size Range of Specimens Included mm.		Average Size mm.		Av. Female Length in Per Cent of Male
		Males	Females	Males	Females	
<i>C. durianus durianus</i>	10	1695-1415	1450-1210	1512	1324	83
<i>C. durianus terrificus</i>	6	1260-1149	1290-1030	1139	1126	95
<i>C. unicolor</i>						
<i>C. basilianus</i>	7	1780-1328	1610-955	1621	1249	77
<i>C. enyo</i>	10	898-763	910-696	796	736	92
<i>C. molossus molossus</i>	10	1253-1117	1060-915	1156	969	83
<i>C. molossus nigrescens</i>	10	1070-810	1053-915	971	939	93
<i>C. adamanteus</i>	7	1320-1217	1023-1045	1631	1319	81
<i>C. cinereus</i>	10	1672-1283	1255-1050	1545	1099	71
<i>C. tortugensis</i>	10	1033-774	990-745	961	901	83
<i>C. lucasensis</i>	10	1306-1213	1127-1017	1243	1050	84
<i>C. ruber</i>	10	1364-1222	1131-1010	1235	1075	84
<i>C. exul</i>	4	940-613	805-602	774	712	92
<i>C. acutistatus</i>	10	1135-1025	1025-937	1064	933	73
<i>C. viridis viridis (Mont.)</i>	10	1320-1140	1120-1015	1209	1037	93
<i>C. viridis oontus (Vinsl.)</i>	10	732-558	553-521	688	537	73
<i>C. viridis abyssus</i>	8	930-777	775-629	971	705	91
<i>C. viridis lutosus</i>	10	1211-1075	1072-879	1135	941	83
<i>C. viridis concolor</i>	10	735-499	615-451	601	526	97
<i>C. viridis oregonus (So. Cal.)</i>	10	1300-1102	1052-360	1163	921	79
<i>C. mitchelli mitchellii</i>	10	939-892	891-816	918	845	93
<i>C. mitchelli pyrrhus</i>	10	1232-1005	1015-775	1092	947	77
<i>C. mitchelli atepensis</i>	10	845-800	734-574	840	740	93
<i>C. tigris</i>	10	915-723	723-545	767	632	92
<i>C. cerastes</i>	10	665-602	767-501	625	660	104
<i>C. polyactis</i>	3	942-725	980-133	325	339	102
<i>C. horridus horridus</i>	10	1196-1020	1130-972	1072	1010	94
<i>C. horridus atricaudatus</i>	8	1600-1300	1475-1025	1372	1136	94
<i>C. lepidus lepidus</i>	4	640-545	540-445	576	474	82
<i>C. lepidus klauberi</i>	10	632-593	587-473	614	513	84
<i>C. triseriatus triseriatus</i>	10	612-513	550-449	555	499	90
<i>C. triseriatus pricei</i>	10	612-527	515-427	562	460	92
<i>C. atepbegei</i>						
<i>C. willardi</i>	7	572-509	565-443	535	499	93
<i>S. rarus</i>						
<i>S. miliaris miliaris</i>	5	515-390	439-390	445	422	95
<i>S. miliaris barbouri</i>	6	550-519	432-395	559	449	90
<i>S. miliaris streckeri</i>	7	493-417	430-415	484	455	94
<i>S. catenatus catenatus</i>	10	787-560	670-547	663	610	92
<i>S. catenatus tergeminus</i>	5	730-523	697-545	645	603	94

the corresponding males, but the largest specimen is a female, which is most unusual.

To check the validity of this deviation we consider all available adult specimens. In cerastes the division between adolescents and adults is at about 400 mm. Falling above this limit we have 135 males and 38 females, which may be presumed to be adults. These have been analysed with the following results: males average 495.3 ± 3.8 mm.; females 523.1 ± 4.5 mm.; the difference is 27.8 ∓ 8.7 . Thus, the difference is 3.2 times its standard error, which is significant, for there is only one chance in 727 that this result is fortuitous. As a further check the available specimens were divided into groups by county areas, and in each area the females averaged longer than the males. We therefore conclude that in C. cerastes, contrary to the condition existing in any other species of rattlesnake, the females reach a larger size than the males, the average adult female being 105.6 per cent of the adult male. The coefficients of variation of these adult cerastes are, males 13.1 per cent; females 11.9 per cent. Whether this surprising deviation of the sidewinder from the male superiority, which seems to be characteristic of the rattlesnakes, is in anyway correlated with the desert habitat of the species and the peculiar method of locomotion which has resulted therefrom I am not prepared to say. This locomotion is the other outstanding peculiarity in which the species differs from its congeners.

It is observed from Table 10 that, with the exception of cerastes, those species represented by not less than ten adults of each sex have female to male length-ratios of from 71 to 98 per cent. The mean of these group ratios is 85 per cent, and I am of the opinion that this figure fairly represents the difference between the largest males and females. This difference, by the way, cannot be accounted for by the increased length of tail of the males, as compared to the females, for this longer tail accounts for only 2 per cent out of the total difference of 15 per cent. All groups except cinereous with 71, and nigrescens with 98 per cent fall between 77 and 94 per cent, which probably approach the true limiting figures. The cinereous and nigrescens ratios have been affected by particular collections.

The groups with less than 10 adults are not sufficiently representative to give assured results. Certainly polystictus, the only species besides cerastes showing a female superiority, is not to be considered a proven deviation like the latter, since the available material is entirely inadequate.

It will be observed that the inferiority of the ten largest females in comparison with the males as set forth in Table 10 is more marked than the corresponding figures for entire adult populations as shown in Table 9. This proves again that sexual dimorphism in size increases with growth, so that the most pronounced difference is found in the largest specimens.

Rattlesnake Lengths--Interspecies Comparisons

We now return to a general survey of the rat-

Table 11
DATA ON RATTLESNAKE LENGTHS (in mm.)

	Minimum Specimen Measured ⁽¹⁾	Estimated Average Size at Birth	Smallest Gravid Female	Maximum Specimen Measured	Maximum Reliable Report ⁽²⁾	Approximate Size of a Large Adult Male ⁽⁴⁾
<i>C. durissus durissus</i>	317	330		1580	1880	1700
<i>C. durissus terrificus</i>	336	305		1230	1400	1350
<i>C. unicolor</i>				920		950
<i>C. basiliscus</i>	296	330		1780		1700
<i>C. enyo</i>	207	225	608	838		870
<i>C. molossus molossus</i>	291	285	703	1253		1200
<i>C. molossus nigrescens</i>	250	280		1090		1150
<i>C. adamanteus</i>	353	350		1820	2440?	2000
<i>C. cinereus</i>	257	310	742	1685	2260	1700
<i>C. tortugensis</i>		250		1038		1000
<i>C. lucasensis</i>	273	290	736	1306		1300
<i>C. ruber</i>	299	300	753	1420	1625	1400
<i>C. exsul</i>		240		940		950
<i>C. scutulatus</i>	220	275	630	1231		1100
<i>C. viridis viridis</i> (5)	212	260	890	1206	1515	1150
<i>C. viridis dunni</i> (6)	248	180	395	732		650
<i>C. viridis abyssus</i>	260	250	684	980		1000
<i>C. viridis lutosus</i>	242	265	643	1211		1170
<i>C. viridis concolor</i>	242	205	522	735		750
<i>C. viridis oregonus</i> (7)	225	275	596	1371		1200
<i>C. mitchellii mitchellii</i>	315	240	797	939		940
<i>C. mitchellii pyrrhus</i>	270	265	786	1295		1100
<i>C. mitchellii stephensi</i>	257	230	674	885		870
<i>C. tigris</i>	307	225	616	815		800
<i>C. cerastes</i>	192	200	434	767 ⁽³⁾		720
<i>C. polystictus</i>	258	240	537	985 ⁽³⁾		950
<i>C. horridus horridus</i>	279	235	897	1195	1550	1250
<i>C. horridus stricaudatus</i>	370	300	1138	1440	1880	1450
<i>C. lepidus lepidus</i>	197	190		648		650
<i>C. lepidus klauberi</i>	168	195	390	693		670
<i>C. triseriatus triseriatus</i>	160	175	441	605		620
<i>C. triseriatus pricei</i>	170	175	301	621		620
<i>C. stejnegeri</i>	282	170		588		600
<i>C. willardi</i>	216	165	481	579		560
<i>S. ravus</i>	194	180		632		620
<i>S. miliarius miliarius</i>	170	160	437	515		530
<i>S. miliarius barbouri</i>	176	170	390	650		630
<i>S. miliarius streckeri</i>	165	165	360	638		620
<i>S. catenatus catenatus</i>	171	210	521	905		850
<i>S. catenatus tergeminus</i>	197	205	623	780		800

- (1) Known to have been born alive and omitting probable freaks.
- (2) Where large specimens have not been properly represented in my series.
- (3) Female; in all other cases the largest measured individual was a male.
- (4) Of the order, say, of the average of the 3 largest males in a group of 100 adults; in the case of *cerastes* the largest are females.
- (5) Montana only (where the subspecies attains its maximum development).
- (6) Winslow area only (where the subspecies is most typical).
- (7) Southern California only (where the subspecies attains its maximum development).

tlesnake measurements available, comprising in excess of 8000, to determine such landmarks as we may, concerning the size at birth, at maturity, and the ultimate length reached by the several species and subspecies. The accumulated data are presented in Table 11.

First there is shown the smallest specimen actually measured, provided it is known to have been born alive, and is not evidently a freak. The data are fairly complete but in a few instances, where relatively few juveniles have been available, it has been clear, both from the rattle and date of capture, that even the smallest specimen is considerably larger than the probable normal size at birth. The next column gives the probable normal size at birth, based on all available broods or juveniles, together with data on the general character of the species. As has been set forth in Table 5, considerable deviations from these figures are to be expected, not only in aberrant individuals, but in brood averages as well. This is especially the case if the mothers have been long in captivity.

In the next column of Table 11 we present rather fragmentary information on the minimum size of females found to contain eggs or embryos. Where adequate series have been available this gives a fair indication of the lower limit of adult size. It must be remembered, however, that the young females carry their first eggs for some 9 months (including 3 to 6 months of hibernation in most species) while still at an age of fairly rapid growth. In general the smallest gravid females have a length of about 60 per cent of the large males and 67 per cent of the larger females. They are about 2 to $2\frac{1}{2}$ times their own length at birth.

Table 11 also sets forth the dimensions of the largest specimens which I have had available for measurement. In a few instances, particularly with respect to the largest species, such as adamanteus, durissus, and cinereous, I have not had access to very large individuals, since they are seldom preserved, and therefore I have supplemented my own records with maximums reliably reported by others, as shown in the next column.

In every species or subspecies, except two, the largest individual proved to be a male. Only cerastes and polystictus deviated from this rule. The former is a real exception, as has already been fully discussed; of the latter I have not had access to a fully representative series.

The largest rattlesnakes are C. adamanteus, C. cinereous, and C. horridus atricaudatus. The first of these is reputed to reach a length of 2440 mm. (8 ft.); the others somewhat less. I have not personally measured any of these monsters. It is possible that some of the published records were based on skins. The following are recent comments on maximum lengths by well-known dealers of long experience:

C. adamanteus. "In the past 12 years I have been in business we have collected a little over 25,000 eastern diamond-back rattlesnakes and the largest specimen that I have personally measured alive was 7 ft. 3 in., weighing 15 lb. This was truly a big snake and looked 9 ft. to the average person.

We have a standing award of \$100.00 offered to anyone who will deliver to us a Florida diamond-back, dead or alive, measuring 8 ft. I advertised this two years ago in all the newspapers of the state and as yet no one has brought one in. A great many skins have been brought in measuring that length, but of course a skin is not accurate." E. Ross Allen, Silver Springs, Florida, by letter March 3, 1937. It should be noted that Dr. R.L. Ditmars has recorded specimens in excess of 8 ft.

C.h. atricaudatus. "The largest canebrake rattlesnake that I recall measuring was 6 ft. 2 in. We get persistent reports of rattlesnakes over 3 ft. long, but unfortunately I have never been able to verify any of them. I have a photograph of an 8 ft. skin, but this probably means a 6 ft. snake." Percy Viosca, New Orleans, Louisiana, by letter March 1, 1937.

C. cinereous. "Checking through my records I find that specimen No. J-6223 received at our farm on July 6, 1926, measured 7 ft. 5 in., exclusive of the rattle. Its circumference was 15.2 in., weight 24 lb. Without a doubt this is the largest western diamond-back ever captured, and considering the fact that we have been in business for more than 34 years and in that time have never encountered a larger specimen, it may be reasonably assumed that this species never measures over 8 ft. in length. The average of the larger specimens varies from 6 ft. 4 in. to 6 ft. 10 in." W.A. King, Jr., Brownsville, Texas, by letter March 6, 1937.

The smallest rattlers are C. willardi and S.m. miliarius. Probably these rarely attain a length of 610 mm. (24 in.).

In addition to these exceptional specimens, Table 11 gives, for each species, the length of what might be termed a "large" adult male; that is, one out of the ordinary, but not so large as to be freakish--say the average of the upper 2 to 4 per cent of the adult male population. With due regard for territorial variations, these figures are somewhat more useful than those comprising the maximum specimens which have happened to come under my observation. However these are judgment figures and no more is claimed for their accuracy than the term implies.

One conclusion which may be drawn from the measurements at birth and maturity is that the larger species have a greater proportionate growth than the smaller. For instance, it will be noted from Table 11 that the ratio of a large adult male to an average juvenile at birth in klauberi is 3.44; in ruber it is 4.67. In cerastes the ratio is 3.60; in oreganus 4.37. These are all species of which large numbers of individuals of all ages have been available for study. While the ratios may not be exactly correct there is no doubt of the fact that there is proportionately less difference in length between the juveniles of the several species than between the corresponding adults, for the juveniles of the largest species are about twice the size of the juveniles of the smallest, while the adults are three times as large; thus there is a greater

growth in the larger species from birth to maturity. The same is true of subspecies; stunted races are proportionately not as small at birth as at maturity. Stunting is in part effective in the post-natal stage and is not the result of a uniform reduction from fertilized egg to maturity.

In Table 11 the ratios between the average dimensions at birth and the "large" adult size are not given, since these ratios were, to a certain extent, employed in determining the two terminal sizes, where a large series of specimens was not available. Hence to cite these ratios as a calculated conclusion would give an inaccurate idea of the validity of the statistics presented.

Length as an Indicator of Age

Whether snakes grow continuously throughout life or whether each individual reaches a maximum size (for that individual) and then stops growing, as do birds and mammals, does not seem to be definitely known. After they reach the adult state, snakes may grow continuously until death, although much more slowly than during the first two or three years of life. This question I propose to discuss further under the rattle section of this statistical study. Assuming that there is continuous growth, and therefore correlation between age and length during the adult stage, it has naturally been asked whether unusually long snakes are not therefore correspondingly old, and whether age cannot be judged from length. To this question our studies of variation do give a definite answer: age cannot be accurately determined from length after the adult state is reached, and the largest snakes are not necessarily the oldest.

This is shown by the fact that no peaks were evident in the size histogram beyond the adolescent stage, thus indicating that individual variation masks age. But we can make the analysis more definite.

We find from rattle studies that in advancing from 11 to 14 complete rattles (which probably represents a year in the life of a snake beginning at age $3\frac{1}{2}$ years) the average male lucasensis grows from about 1080 to 1123 mm., an increase of 43 mm. We now make two assumptions, both of which favor the determination of age by size: we assume a growth in the following year of 43 mm. (there is evidence that it is less); and we assume that each age-class is distributed as to size in accordance with the normal curve of error (there is evidence that the actual curve is somewhat flatter). We have already found that the coefficient of variation of a single age-class is at least 7 per cent in youth and there is every reason to believe that this increases rather than decreases with age, just as it has been shown to increase from the juvenile to the adolescent stage. Nevertheless we assume that the coefficient of variation of a single age-class of adults is 7 per cent. With this variation the snakes of an age-class averaging 1123 mm. will have the distribution 1123 ± 53 , that is, half of them will vary between 1070 and 1176 mm., one quarter will be smaller than 1070 and the remainder larger than 1176 mm. The snakes one year older will average 43 mm. larger (with the favorable assumption that has been made) and the distribution will be 1166 ± 55 mm. Thus more than one quarter of the younger snakes will be longer than the

Table 12

COMPARISONS OF LENGTHS: PLATTEVILLE AND PIERRE SERIES
(All lengths in millimeters)

	Platteville Series	Pierre Series	Ratio Platt./Pierre
Number of specimens available	861	732	
Minimum length, male	246	272	.90
female	248	255	.97
Average juveniles, male	304	339	.90
female	291	334	.87
Average specimen over 400 mm., male	712	768	.93
female	674	740	.89
Average adult*, male	776	862	.90
female	737	822	.90
Smallest gravid female	588	683	.86
Average 5 largest males	975	1055	.92
females	857	965	.89
Largest individual, male	1015	1076	.94
female	863	1020	.85

* Above 650 mm. for Platteville and 705 mm. for Pierre series;
for derivation of these limits see the text.

average size of the next older year class. In general, in a series of overlapping normal probability curves where the separation of successive peaks is less than half the interquartile range of one curve, it can be shown that the chance of properly allocating a single individual to its true year-class is less than one in two.

Thus increased length is more likely to be the result of individual variation than of increased age, even under these favorable assumptions; and I conclude that mere size is not of itself a definite indication of great age.

Variations within a Subspecies

One who has had the occasion to handle large numbers of snakes from various regions soon becomes convinced that there are size differences even within a subspecies--that the snakes from some areas average larger than from others. In certain instances these differences are quantitatively so great that they justify subspecific differentiation, especially if validated by modifications in other characters as well. A typical example is C.v. nuntius, especially in the immediate vicinity of Winslow, Arizona; these snakes have differentiated from the obviously parent form, C.v. viridis, not only in size, but in color and lepidosis.

Herpetologists have not been as ready to accept mere size as a character justifying subspecific separation as have mammalogists and ornithologists because of the lack of consistency in size (high coefficient of variation) amongst adult reptiles as compared to the mammals and birds.* This may result in part from a presumed continued growth in the reptiles after the adult state is reached.

I do not suggest a change in this non-recognition of mere size as a subspecific differential, although separation may be justified in some extreme island or other isolated forms. However I do think it worth while to demonstrate that these size differences, which might be considered only unfounded opinions, actually occur in closely contiguous populations; for they can be proved real and significant, if sufficiently large population samples be available. This is the beginning of racial differentiation, which may, through subsequent divergence and isolation, become specific.

This type of incipient territorial variation may be demonstrated by a study of the Platteville and Pierre series of C.v. viridis. Here the differences would not be apparent were there only a few specimens to compare. But

* As an example of the consistency in length in a series of adult mammals, measurements of body length (exclusive of tail) were secured on 98 male and 93 female kangaroo rats (Dipodomys merriami simiolus) from the vicinity of La Puerta, San Diego Co., Calif. These are in the collection of the San Diego Society of Natural History. The coefficients of variation are: males 4.95 per cent; females 5.27 per cent. These results are to be compared with 3 to 14 per cent in an adult population of rattlers. Thus these rats adhere more closely to the mean than do the snakes.

Table 13

DIFFERENCES BETWEEN TWO POPULATIONS OF Crotalus viridis viridis

Averages

	Platteville Series	Pierre Series	Difference*	Significance ^φ
Scale Rows	26.47 ± .02 [#]	26.52 ± .03 [#]	-.055 ± .0525	1.05
Ventrals - Males	178.87 ± .10	176.77 ± .12	2.082 ± .223	9.32
Ventrals - Females	185.80 ± .11	184.02 ± .12	1.780 ± .247	7.20
Caudals - Males	26.23 ± .05	26.13 ± .05	.094 ± .103	.93
Caudals - Females	20.36 ± .05	20.08 ± .06	.235 ± .115	2.05
Supralabials	14.76 ± .02	14.88 ± .02	-.122 ± .033	3.68
Infralabials	15.87 ± .02	15.81 ± .02	.061 ± .037	1.65
Scales before Supraoculars	23.28 ± .12	20.76 ± .13	2.521 ± .259	9.74
Min. Scales between Supraoculars	3.45 ± .02	3.00 ± .02	.446 ± .040	11.15
Body Blotches - Males	42.25 ± .11	43.77 ± .12	-1.525 ± .239	6.38
Body Blotches - Females	42.95 ± .11	43.75 ± .12	-.797 ± .246	3.24
Tail Rings - Males	9.64 ± .04	10.08 ± .05	-.443 ± .919	.48
Tail Rings - Females	7.39 ± .03	7.48 ± .04	-.091 ± .080	1.13

* Negative sign means the Pierre series is higher than the Platteville.

^φ Based on the standard, not probable, error of the difference.

[#] In calculating the significance of the differences the means and their probable errors were carried one decimal place further than here shown to assure numerical accuracy.

good series are available from both places, there being 861 and 732 individuals respectively. These two populations are so similar that even the veriest "splitter" would consider them identical; yet even in these groups, separated by about 370 miles of prairie and living in ecological surroundings not widely dissimilar, differentiation has already begun, not only in length but in other characteristics as well.

Table 12 presents some of the principal landmarks of length in these two series of snakes. It will be seen that in these criteria, without exception, the snakes of the Pierre series are larger than the Platteville.

In this table the juvenile and adolescent groups are again divided at 400 mm. as was done before with the Platteville series alone. While it might be consistent to divide the Pierre series at a slightly higher figure, say 430 mm., this would result in transferring only 2 males and 2 females to the juveniles from the adolescents, and the change in the averages would be negligible. The main point is that there is a natural break in both series between 380 and 440 mm., so that there is almost no confusion between juveniles on the one hand, and adolescents plus adults on the other.

That the juvenile differences are real is shown by the following statistics of average length:

	<u>Platteville</u>	<u>Pierre</u>	<u>Difference</u>	<u>Significance</u>
Males	303.18±1.62	339.00±2.09	34.82±3.91	8.9
Females	291.50±1.50	333.67±1.96	42.17±3.66	11.5

However, it might be argued that the juveniles, being at a period of relatively rapid growth, the average difference in juvenile length between the two series could be the effect of measuring the larger series when somewhat older than the smaller. But the adolescents plus adults, including all specimens above 400 mm., cannot be subject to such a doubt, for they are, proportionately, growing more slowly. Their average lengths and differences are found to be as follows:

	<u>Platteville</u>	<u>Pierre</u>	<u>Difference</u>	<u>Significance</u>
Males	711.97±4.17	768.38±5.90	56.41±10.68	5.3
Females	674.05±3.64	740.00±5.20	65.95±9.39	7.0

Thus the differences are seen to be in excess of 5 times their standard errors, which again are highly significant.

Carrying the comparison further we can make a rough differentiation of adults from adolescents as follows: We have previously shown in the Platteville series that there is a rapid increase in female gravidity at 640 mm. (Occ.Pap.No.1,p.17). Remembering that the males are slightly longer than the females of similar age we will make an arbitrary division between adolescents and adults at 650 mm. This will include, amongst the adults, a few oversize adolescents; and correspondingly, it will exclude some of the lagging or stunted adults; but the results will still be comparable if we use the same method for both series. In the Platteville series we find that, of all the adolescents

Table 14

COEFFICIENTS OF VARIATIONS OF STANDARD CHARACTERS - PER CENT

Species	Territory	Specimens	Scale Rows	Ventrals*	Caudals*	Supralabials	Infralabials	Scales on Crown [#]	Body Blotches*	Tail Rings*
C.enyo	Lower Calif.	61	3.1	1.7	6.1	5.8	6.2	22.1	7.0	19.2
C.molossus	U.S.	99	4.0	2.3	6.3	6.5	6.6	43.4 [#]	11.0	-
C.cinereous	Arizona	216	3.7	2.9	7.5	5.6	5.8	19.9	5.9	16.2
C.cinereous	Texas	238	3.0	1.9	6.7	5.9	6.2	19.7	6.9	15.0
C.cinereous	All	620	3.8	2.6	7.1	5.9	6.3	21.3	6.6	17.0
C.lucasensis	Cape S.L.	276	3.7	2.0	5.7	6.0	6.0	19.2	7.0	12.2
C.ruber	All	252	4.2	2.0	8.6	5.9	5.7	23.0	7.9	17.1
C.scutulatus	Calif.-Ariz.	335	3.0	2.3	7.4	5.9	6.6	20.4	7.5	16.5
C.viridis viridis	Platteville	833	3.8	1.7	6.7	6.1	6.4	22.1	7.7	13.0
C.viridis viridis	Pierre	673	3.8	1.8	6.3	6.1	6.3	23.4	7.5	14.2
C.viridis lutosus	All	346	3.5	2.4	7.5	6.1	6.3	21.3	7.8	14.5
C.viridis oreganus	Sou.Calif.	598	3.6	2.1	9.0	6.0	6.2	20.2	7.0	21.8
C.viridis oreganus	Pateros	202	3.5	1.9	6.1	5.6	5.6	20.0	8.6	15.2
C.viridis oreganus	All	1140	3.7	2.6	9.3	6.0	6.4	21.3	8.3	22.8
C.mitchellii pyrrhus	All	166	4.2	2.1	7.8	6.6	6.3	19.1	8.3	18.0
C.cerastes	All	259	5.1	3.0	8.2	6.5	6.6	18.0	7.6	19.9

* Where there is sexual dimorphism, the coefficients have been separately calculated for each sex and then averaged.

♂ Scales on top of head anterior to supraoculars and intersupraoculars.

This high figure is the result of the peculiar character of these scales in this species.

and adults together, 63 per cent fall into our arbitrarily fixed adult class. Now if we take the upper 63 per cent of the Pierre series as probable adults we find that this causes a corresponding break between adults and adolescents at 705 mm. With these division points we find the significance between the two series of probable adults as follows:

	<u>Platteville</u>	<u>Pierre</u>	<u>Difference</u>	<u>Signifi-</u> <u>cance</u>
Males*	776.16 \pm 3.52	862.16 \pm 4.46	86.00 \mp 7.87	10.9
Females	735.61 \pm 2.74	822.00 \pm 3.38	86.39 \mp 6.42	13.5

With differences of this order compared with their corresponding standard errors there can be no question as to their reality. Thus conclusive evidence has been presented that the Pierre snakes average longer than those from Platteville throughout life. The magnitude of this difference is about 10 per cent. Even the rattle shows the same result: 448 Platteville buttons average 5.1 mm. in width, while 321 Pierre buttons average 5.6 mm. and the dispersion is such that the difference is highly significant.

At this point it will be interesting to show the extent to which these two populations have diverged in other characteristics. I therefore anticipate certain studies, which I hope eventually to publish, on the stability of characters used in herpetological classification, and present in Table 13 the differences between these two population groups in respect of some commonly used scale and pattern characters.

Here we see differentiation definitely begun, for the difference between the two, although small, is significant in more than half the characters. The average difference of only about 2 ventral plates in each sex may seem negligible; but actually, because of the large samples available, these differences are more real than average differences of 10 or 15 ventrals might be if only a dozen snakes were at hand from each area, as is so often the case in our taxonomic studies. For with such large series of viridis the chance that this difference of two plates is the result of the hazard of sampling, and does not really exist in the general populations, is only one out of many billions. Positive results of this character cannot be secured with small samples, and a mere statement of differences between averages does not tell the whole story.

Length Compared with Other Differential Characters

In order to show how length, as a variable in a homogeneous group, compares in consistency with other characters used in classification, Table 14 is presented. This sets forth these characters in terms of their coefficients of variation. Both territorially homogeneous and wide-spread groups have been used as examples. A rather notable uniformity in the coefficient for each character is evident. In comparing these with length it is to be remembered that the studies thus far presented indicate a coefficient of variation of 10 to 12 per cent in the lengths of an adult

* No attempt should be made to draw intersex comparisons here; the arbitrary setting of the same lower limit for males and females is unfair to the former.

population segregated between the sexes. Therefore length is more variable than most of the scale characters. And owing to the change which an individual experiences in this character through life it is not particularly valuable in classification, for it can only be used when large population samples are available.

But I am not attempting to prove that Colorado and South Dakota viridis are separate subspecies, either by the use of adult length or other characteristics. A real difference between them has been shown mathematically; but any system of classification which required 500 specimens from an area before its population could be classified, would be worse than useless. The presence of real differences between adjacent populations is probably more universal than is generally realized, but these differences should not be used as a basis of nomenclatorial distinction unless some of them are of practical use. To differentiate subspecies we should have available one or more characters which will successfully segregate a large proportion of the individuals of the two groups taken as individuals. But the statistical approach should not be neglected in verifying the validity of the conclusions.

Ecological Variations

Having shown statistically the extent of a territorial difference in size within a subspecies we may mention a few other outstanding subspecific and specific instances of size differences and speculate on their possible causes.

In general the duration of seasonal activity does not seem to be a controlling factor, although possibly effective in some instances. Oreganus in southern California is a larger snake than in central Washington; cerastes is larger in Imperial County than in Inyo County, California; atricaudatus is larger in Louisiana than horridus in the upper Mississippi basin; and in each case the larger form has a longer season. But, on the other hand, viridis is larger in the northern part of its range than in the southern; pyrrhus is larger than mittelli; catenatus grows to a larger size than tergeminus. In the latter three cases the smaller snake has the longer seasonal activity, so there is no uniform result from this variable factor.

It is true that widely ranging forms tend to be smaller in the mountains than in the lowlands. Thus cinereous and scutulatus are both smaller in the vicinity of Prescott, Arizona, than in the plains to the south and west; oreganus above 6000 ft. altitude in southern California shows a declining size as it approaches its limit at about 11000 ft. But there are other species, of more restricted adaptability, which flourish only in the mountains, as witness such forms as pricei and klauberi in their island-like montane habitats in southeastern Arizona.

Desert conditions cause stunting in some species; thus ruber is a somewhat smaller snake on the edge of the Colorado desert than in the coastal foothills; and the same is true of mittelli in western Arizona as compared to the same snake in the Upper Sonoran Life Zone of the peninsula

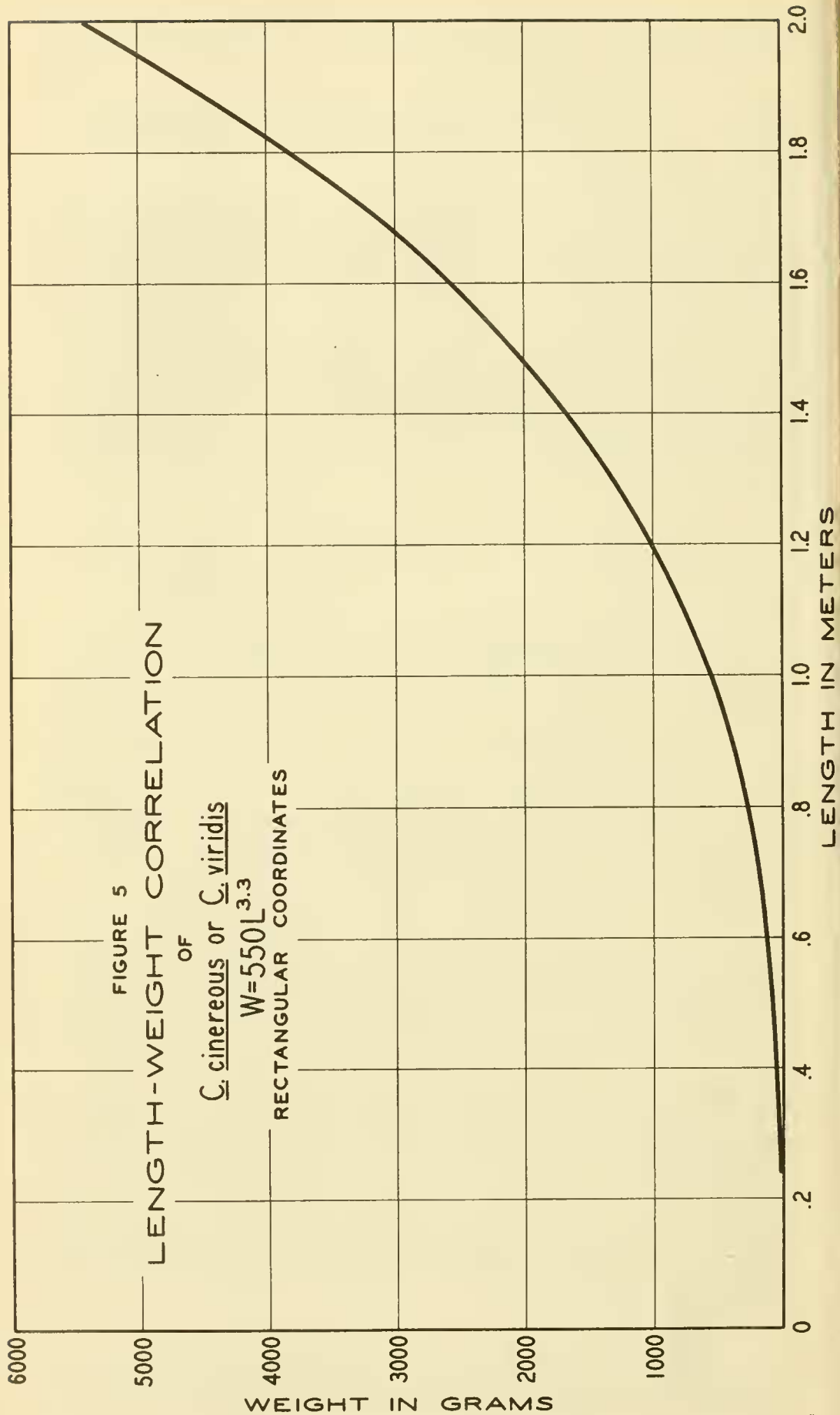
range of southern California. On the other hand cerastes is sharply limited to the desert and is of smaller size on the periphery of its range.

It cannot be food alone which causes these fluctuations in size; rodents are probably as plentiful in northeastern Colorado as in Montana; the lizard feeders pricei and klauberi are not prevented from ranging further down the mountains by lack of food, for lizards are more plentiful in the lower altitudes. Thus the causes of these habitat preferences and morphological variations are obscure. One fact is outstanding: the species which are most sharply limited in ecological adaptability, and therefore in range, are most constant in form. Compare for instance the constant adamanteus, ruber, and cerastes with such variable forms as horridus, oreganus, and pyrrhus. We would naturally presume that the morphological variability is the result of variations in habitat; but it does not follow with certainty that this is cause and effect, for oreganus and pyrrhus are not only variable when comparing specimens from different sections of their ranges, but are highly diversified at any one locality.

Island forms are always of interest. Some of the island rattlesnakes are conspicuously stunted: for example tortugensis is a stunted form of cinereus, its nearest relative on the mainland; so also is exsul a stunted offshoot of ruber. The molossus on San Esteban Island is stunted. Probably most conspicuous of all are the stunted oreganus found on South Coronado Island, a rocky islet only a few miles from the mainland near San Diego. These snakes differ from the coastal form to such an extent that they would certainly warrant subspecific recognition were there any differences of scutellation comparable to the difference in size. Thus there are available 8 adult* island males which average 603 mm. (min. 516, max. 683) and 14 adult females average 547 mm. (min. 492, max. 647). Needless to say these specimens are pigmies compared to the mainland adults, which are nearly twice as long and about eight times as bulky.

But diminution in size on islands is not universal, for the pyrrhus on Ángel de la Guarda are the largest known of that wide-spread form. This is the more remarkable since ruber on the same island seems to be somewhat smaller than on the mainland, although not conspicuously so. Cinereus on Tiburón seems to be about normal, as is also the case with lucasensis on San José and Santa Margarita. There are available hardly enough ruber from South San Lorenzo, San Marcos, and Monserrate Islands, or enyo from San Francisco, Carmen, and Isla Partida to prove anything with reference to size. The smallest gravid female oreganus (394 mm.) out of more than 1400 specimens is from Morro Rock, from which islet only two specimens are available; this can hardly be a coincidence, so it is probable that this rock is inhabited by another stunted strain. We conclude that, while diminution in size in races of rattlesnakes isolated on islands is frequent, it is by no means universal; and in at least one instance the contrary condition is the fact.

* The adult state may be judged from the condition of parallelism in the proximate rattles.



Length-Weight Correlation

In an endeavor to learn the character of the correlation between the length and weight of rattlesnakes, a number of specimens were weighed and measured immediately after killing, but prior to preservation. Most of the weights were secured on an accurate torsion balance. A few measurements and weights of live specimens were recorded.

To test the usefulness of preserved material, a series of specimens were weighed before and after preservation and the results were compared. The effect of the preservative was found to be so variable that weights of preserved specimens should be considered entirely undependable as criteria of live weight, and therefore none has been used.

That there is a correlation between length and weight is, of course, certain, for this must be the case in any animal whose form remains approximately constant during growth. The question is the nature of this relationship and its consistency; that is, the character of the average length-weight regression curve and the extent of the dispersion of individual specimens about that curve. Also we should determine whether there is a significant sexual dimorphism.

In attacking a problem of this nature a preliminary visual study is advisable. We find, by taking the lengths and weights of a representative series of any species and plotting them on rectangular coordinates, that we have a curve which shows rapidly rising increments of weight with equal increments of length; the curve is apparently parabolic in form (Fig.5). This is to be expected, since if the form and specific gravity remain constant during growth, the weight will vary with the cube of the length. The data were therefore transferred to paper having logarithmic coordinates in both directions and it was found that a straight line relationship was indicated; thus the curve is of the form $W = CL^P$, where C and P are constants, since double logarithmic coordinates reduce such a curve to a straight line. Although the scatter is considerable, the deviations seem to be random, hence they are the result of individual aberrations rather than the non-suitability of the equation.

Not only does the logarithmic expression reduce the curve to a straight line, and thus simplify the investigation of the relationship, but it is also noted that the scatter is now apparently uniform along the curve, where before, with rectangular coordinates, it was much greater amongst the adults than the juveniles. Remembering that equal deviations represent constant deviation ratios at any point in a log-log diagram, this means that deviations in weight from the average remain relatively constant in proportion throughout life. Thus the logarithmic device rationalizes both the relationship and the scatter.* A dispersion of this type is to be expected; certainly if a deviation of 8 per cent, or 8 grams, for example, were found to be the average deviation at a normal weight

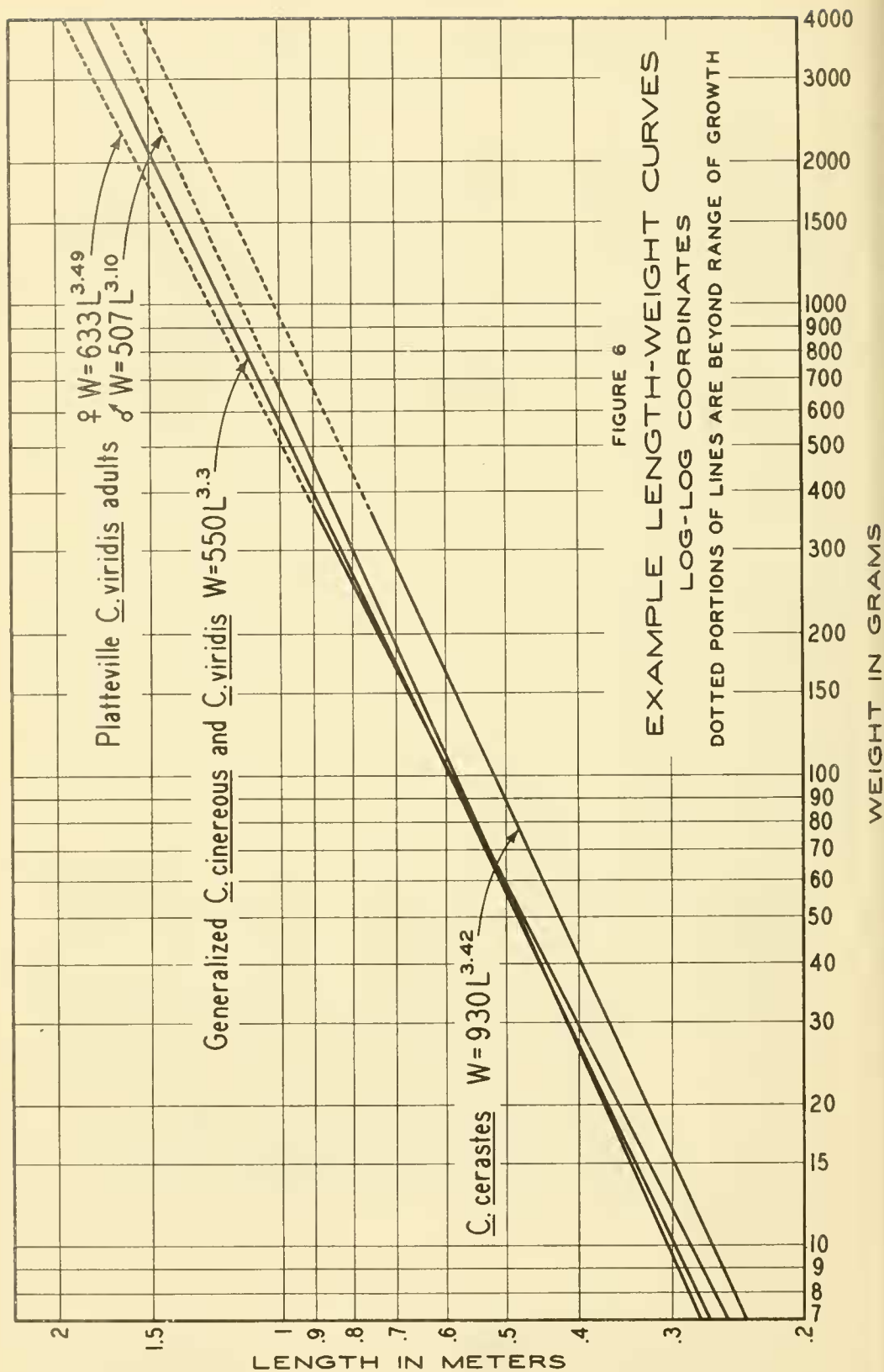
* This method assumes a geometric rather than an arithmetic dispersion around the regression line. Mills, op.cit., p.475.

Table 15

LENGTH-WEIGHT CORRELATION

Species or Group	Number of Specimens	C	P	r	S
<u>I Juveniles and adults</u>					
C.adamanteus	14	560	3.16	.963	.0533
C.cinereous	65	535	3.32	.975	.0843
C.lucasensis	33	510	2.91	.969	.0742
C.ruber	61	577	3.30	.986	.0783
C.v.viridis-Platteville	818	496	2.93	.990	.0725
Pierre	338	468	2.94	.991	.0715
Montana	67	593	3.36	.989	.0991
Nebraska	24	535	3.18	.985	.0606
C.v.oreganus-S.D.County	114	675	3.00	.983	.0984
C.m.pyrrhus	17	737	3.24	.987	.0935
C.cerastes	22	930	3.42	.992	.0633
<u>II Adults alone</u>					
C.v.viridis-Platteville	594	545	3.20	.948	.0721
Pierre	223	472	2.98	.973	.0695
C.v.oreganus-S.D.County	76	698	3.10	.990	.0638
<u>III Juveniles alone</u>					
C.cinereous-San Patricio*	139	395	2.73	.739	.0539
C.v.viridis-Platteville	224	358	2.68	.796	.0300
Pierre	118	364	2.71	.877	.0500
Montana*	44	664	2.70	.642	.0578
C.v.oreganus-S.D.County	46	820	3.21	.936	.0504
<u>IV Adults with sexes separated</u>					
C.v.viridis-Platteville ♂	315	507	3.10	.960	.0639
♂	279	633	3.49	.945	.0722
Pierre ♂	115	457	2.90	.981	.0628
♀	108	498	3.11	.967	.0738
C and P are the constants to be used in the length-weight equation: $W = CL^P$ where W is expressed in grams and L in meters. r is the coefficient of correlation and S the standard error of estimate, both having reference to the dispersion in logarithmic terms about the straight line $\log W = P \log L + \log C$					

* These young, being of special quality, are not included in the series in Group I.



of 100 grams, we would not expect to find the same deviation of 8 grams at a weight of 1000 grams, but would expect 80 grams, or 8 per cent as before. And this condition is found to agree substantially with the facts.

Having determined the form of the correlation curve our next step should be to calculate the equations of those species for which data may be available, and to find the extent of group and species differences. Such an investigation was therefore carried out on all species, or territorial groups, of which weights of representative series at various ages were at hand, the results being set forth in Table 15. Where 25 or fewer specimens were available the least-squares method was employed; otherwise the product-moment method, with grouped data, was used.* The raw data thus used are too voluminous to be included here, but Table 16 is presented as a sample to show the method of grouping, and to indicate the approximate consistency of the correlation. This table covers the Platteville series as a whole. It should be understood that with groups having smaller size-ranges (juveniles for example) the grouping was by narrower class-limits.

In Table 15 there are set forth the constants applicable to the equation $W = CL^P$ (where the length L is expressed in meters[♂] and W is the weight in grams) for a number of species, and for several other groups segregated as to locality, size, or sex. In addition, to give an indication of the extent of the dispersion, the coefficient of correlation (r) and the standard error of estimate (S) are also shown. However, it is to be remembered that these latter refer to the equation in its straight line form, $\log W = P \log L + \log C$. Similarly, Fig. 6 shows several of the equations plotted on log-log coordinates to show their general trends, and how differences in C and P affect these trends.

In discussing the results shown in this table, I wish to draw attention to various conditions of the snakes weighed which affect the determinations and tend to reduce the accuracy of the constants found for certain groups. First it should be noted that there is sexual dimorphism and therefore in the groups wherein the sexes are combined the constants will be affected by the sex proportions. Similarly, in devising a body-weight curve, all size-classes should be represented in approximately equal number; concentrations, such as overly large proportions of juveniles, may modify the determination, if this particular group tends to deviate from the normal. The Platteville and Pierre series, when including the juveniles, have been so affected; for this reason the curves based on adults alone are believed to represent the average situation more accurately. Finally, there are such matters as season of capture, availability of food, gestation, and the unnatural

* See Mills, P. 401, or any similar statistical text.

♂ The reason for the seeming inconsistency in expressing L in meters in this equation and employing millimeters elsewhere is the inconvenient size of C when using millimeters. For example the equation $W = 530L^{3.4}$, L being expressed in meters, becomes $W = 0.0000003659L^{3.4}$ when L is expressed in millimeters.

conditions of captivity. In the last regard the lucasensis and Pierre viridis series were adversely affected, which I believe explains the low constants in these two cases. Taking into account these several effects, I am of the opinion that the equation $W = 550L^{3.3}$ fairly represents the average length-weight correlation of the snakes of the cinereous and viridis groups in the wild. The results from the small series of pyrrhus and cerastes indicate that, since both C and P are high, these are chunkier, heavier-bodied snakes than cinereous or viridis. Such indeed is their adult appearance.

The fact that the exponent P exceeds 3 indicates that rattlesnakes do not retain a constant shape throughout life (assuming a constant specific gravity) but become somewhat heavier-bodied or stouter with age.

Before proceeding to an investigation of the extent and character of the dispersion about the regression lines, and whether there is sexual dimorphism, I think it well to translate the average equation of $W = 550L^{3.3}$, which is taken as representing the weight-length correlation of such important species as viridis and cinereous, into abbreviated tables which will make the relationship more readily apparent.

<u>Metric Measure</u>		<u>English Measure</u>	
Length, mm.	Weight, grams	Length, ft.	Weight, lb & oz
250	5.7	1	0.4 oz
300	10.4.	1½	1.5 "
350	17.2	2	3.8 "
400	26.8	2½	7.9 "
500	57.2	3	14.5 "
700	170	4	2 lb 5 oz
1000	550	5	4 " 14 "
1500	2096	6	8 " 14 "
2000	5417	7	14 " 13 "
2500	11310	8	23 " 0 "

The above two tables, although based on the same equation, are entirely separate; no attempt should be made to read across from one to the other. The outstanding point evident from these tables is the rapid increase in weight, for relatively small increases in length, as the larger sizes are approached.

A point to be remembered in comparing two equations of the form $W = CL^P$ wherein C and P are different, is that W does not increase in all sizes of snakes as C and P increase. If C remains constant, lower values of P result in higher values of W in lengths below 1 meter, since when L is less than 1, log L is negative. The extent to which W changes with small changes in C and P is shown by the following figures for two slightly different equations:

<u>L in meters</u>	<u>Value of W in grams</u>	
	$W = 550L^{3.3}$	$W = 580L^{3.4}$
0.3	10.4	9.7
0.4	26.8	25.7
0.5	57.2	55.0
0.7	170	174
1.0	550	580
1.5	2096	2302
2.0	5417	6120

Another point to be noted with respect to these equations is that C is the weight in grams of a snake 1 meter long, since when $L = 1$, $W = C$.

We see from these sample tables why long rattlers look so huge. A six-foot rattlesnake has almost twice the bulk of one 5 feet long. While a racer $7\frac{1}{2}$ feet long, because of its attenuated form, would not look like a large snake, particularly if coiled in a cage, a heavy-bodied snake such as a rattler of similar length looks enormous. He has a greater bulk than a king-cobra twice as long. It should be understood, however, that while a comparison of the bulk of a short and a long rattler is accentuated by the value of P in excess of 3, this does not account for the stoutness of the rattler as compared to a racer. This is primarily due to a high value of C rather than of P. Racers and cobras may also increase in weight more rapidly than the cube of their lengths; this is a condition which I have not investigated.

Fluctuations in Weight

The regression curve of weight on length, $W = CL^P$, is interesting as showing a certain correlation in nature, but it is doubtful whether it will prove useful in taxonomy, as are, for instance, curves of head and tail proportions. Possibly when length-weight measurements are available for many additional series, interspecies trends may come to light which have not been evident in my limited material. As a practical guide for making a rough calculation of the probable weight of a rattlesnake, when the length is known, the equation is of possible use. Such a calculation should be made using the equation in its straight line form, $\log W = P \log L + \log C$.

But primarily the equation is of interest as a description of rattlesnake growth--a fact of natural history. As such it is worth while to determine how closely the average snake adheres to the regression line representing his species, and what will be the probable discrepancy if the equation is used to calculate the weight from the length. In general the answer is to be found in the last column of Table 15, giving S, the standard error of estimate. The coefficient of correlation (r) is not to be given much weight as its value depends to a considerable extent on the distribution of lengths of the specimens which happen to make up the series investigated.

In an ordinary correlation study the standard error of estimate is theoretically the standard deviation of the dependent variable at any fixed value of the independent variable, assuming a large number of samples concentrated at that point. In the present instance, because of the change of the equation to its logarithmic equivalent, the standard error given in the table must be translated into a percentage figure.* We find that in the Platteville series half of the specimens will fall between .89 and 1.12 of the value determined from the curve; 68 per cent will fall between .84 and 1.18; 95 out of 100 will fall between .72 and 1.40. In other words there is an even

* For the method used see Mills, op.cit., p. 460.

chance that the true weight of any single specimen of this series will not be more than 12 per cent above or 11 per cent below the weight calculated from the curve. In a similar way percentages falling within and without any limits may be determined for any value of S. As the values of S in Table 15 do not vary to a great extent, the above determinations with respect to the Platteville series, in which more specimens have been available than any other, probably represent closely the extent of the variation in all these species of rattlers. I am of the opinion that 12 per cent is a close approximation to the probable error of estimate, or 18 per cent to the standard error.

In order to indicate the results thus obtained, uncomplicated by the logarithmic feature, I determined from the equation $W = 496L^{2.83}$ the theoretical weight of each specimen of the Platteville series and then calculated the ratio of the actual to the theoretical weight. The results are summarized in the following table of deviations; the first column showing the group limits, the second the number of specimens falling in each group:

Ratios of actual to theoretical weight.

.50- .59	1
.60- .69	9
.70- .79	38
.80- .89	108
.90- .99	204
1.00-1.09	173
1.10-1.19	143
1.20-1.29	32
1.30-1.39	40
1.40-1.49	13
1.50-1.59	6
1.60-1.69	1

It is noted that the distribution about the regression line is approximately normal, although slightly skewed, with a longer tail toward the higher ratios. The coefficient of variation of this distribution is 16 per cent.

Females should vary more than males because there is a gradual increase in weight during gestation and a sudden decline when their young are born. This is found to be the case in both the Platteville and Pierre series where S is greater for the females than the males. Taking the Platteville series, for example, we find that half the males will fall between 1.104 and .906 of the calculated value, but half the females will fall between 1.119 and .894, thus showing a wider dispersion.

Sexual Dimorphism in Weight

From Table 15 we have the following data on adult* snakes:

* We have made the usual division at 400 mm.; thus the equations include the adolescents. The omission of the adolescents does not materially change the result. The Platteville series from 532 mm. up (thus comprising adults almost exclusively) has the following equations: males $W = 508L^{3.10}$; females $W = 642L^{3.51}$. Thus the female equation is changed slightly by the exclusion of the adolescents; the male equation remains virtually unchanged.

Platteville males	W = 507L ^{3.10}
females	W = 633L ^{3.49}
Pierre males	W = 457L ^{2.90}
females	W = 498L ^{3.11}

There is evident here an increase in both C and P in the females over the males. The Platteville series probably gives a better indication of the true curve for this species, since this series contains a larger proportion of autumn specimens (not attenuated by hibernation) and there was a shorter period of captivity before they were weighed. Hence, I am of the opinion that the Platteville series, with about twice as many autumn as spring measurements, have constants closely approximating the normal figures for the prairie rattlesnake during its active season. The Pierre statistics, while not so accurate as to trends, are still valuable for intersex comparisons.

That the coefficients P are significantly different as between males and females, is shown by the following figures:

Values of Coefficient P

	<u>Males</u>	<u>Females</u>	<u>Difference</u>
Platteville	3.096 ± .0511	3.487 ± .0720	.391 ± .00519
Pierre	2.903 ± .0481	3.107 ± .0791	.203 ± .00878

Since the difference is, in each case, many times its standard error, there remains no doubt as to the significance of this sexual difference in exponents. The differences in the constant C are less significant.

An interesting derivation is the ratio between the weights of adult snakes of similar lengths but opposite sexes, which can be found by dividing one equation by the other. Thus we have for the Platteville series a female to male ratio of $633L^{3.49}/507L^{3.10}$ or $1.25L^{.39}$; for the Pierre series the corresponding result is $1.09L^{.21}$. To determine where the sex curves cross we equate these ratios to 1 and solve for L. We find that the Platteville curves intersect at L = 565 mm. and the Pierre at L = 664 mm. This indicates that adolescent males are heavier than females of the same length, and that the contrary is true amongst the adults. It is interesting to find that in both of these series the lengths at which the females begin to be heavier than the males closely correspond to the sizes of the smallest gravid females; for the figures are 565 mm. (weight criterion) and 538 mm. (gravity) in the Platteville series, and 664 and 633 mm. respectively in the Pierre series. We have here an interesting confirmation of the lower limits of adulthood previously determined. But it must not be thought that the females are heavier merely because of the eggs which they carry; they are actually stouter than the males, which may be in part the result of their reduced activity. Based on the Platteville data, at the maximum size reached by the females (900 mm.), they are about 20 per cent heavier than the males of the same length. Of course the males grow to a greater length than the females and hence eventually exceed them in bulk.

Is this sexual difference in weight really significant? The answer depends on the age, for obviously there

is no difference at the point where the regression curves cross. But the difference increases through the adult stage, and at the largest size reached by the females (say 900 mm.) we have average weights of 438.1 g. and 365.6 g. for the females and males respectively. Using a coefficient of variation of 18 per cent, which is a safe figure based on our studies of the standard error of estimate, we find the difference of the mean weights at 900 mm. to be 72.5 ± 6.0 g. The difference is 12 times its standard error and unquestionably significant.

It might be thought that much of the sexual dimorphism in weight can be attributed to the longer tail of the male. It is true that this does account for a part of the sex difference. It must be remembered that the female tail is shorter than the male, the ratio of the tail to over-all length in the Platteville series averaging 0.074 (range 0.060-0.093) in the males, and 0.054 (range 0.040-0.072) in the females. Thus in a pair of snakes each 900 mm. in length, the male would have a tail length of about $66\frac{1}{2}$ mm. and the female $48\frac{1}{2}$ mm., a difference of 18 mm.; and, for equivalent body lengths, we should compare a male 918 mm. long with a female of 900 mm. By this method of comparison the weight difference between the sexes is only 12 per cent in favor of the females, instead of 20 per cent when comparing on a basis of equal length over-all.

Weight of Young Snakes

Table 15 indicates that in the juveniles of the Platteville, Pierre, and Montana viridis, and San Patricio cinereous series, the exponential constant P is lower than amongst the adults of the same series. This is not true of the oreganus series, which has the same type of exponent as the adults. I think the explanation is to be found in the character of the former series--the fact that they are what might be called dispersion groups instead of growth groups. These four groups (the viridis and cinereous) are chronologically concentrated; thus they represent variations surrounding a mean at one age, rather than stations along a trend-line of growth, as does the oreganus series. The Montana group was measured immediately after birth; the San Patricio series several weeks after, but they had had no food. A few of the Platteville and San Patricio series, collected at the snake dens, may have secured food between birth and hibernation,* but still they are chronologically a unit. With these food limitations, prenatal, postnatal or both, the larger snakes are likely to be somewhat attenuated and P will be less than 3; for if a snake grows more rapidly than his brother but secures no more food, he will be thinner. Thus the conditions of correlation in these groups are not of the same character as in groups representing all phases of growth; and it is to be expected that even if the mean of the group falls in the general regression curve for that species, the group itself is likely to have a regression line at an angle with the main species regression. But in the oreganus series we have specimens caught at all periods between birth and hibernation, and

* Mr. C.B. Perkins tells me that possibly 10 per cent of the Platteville juveniles caught in the autumn, disorged Holbrookia (lizard) remains.

others from various dates in the spring, after they had secured food. In a small series caught and examined in late March, half had already secured either lizards or mice. So the oreganus series indicates a true life trend, rather than a group dispersion as indicated by the other juveniles. The constants determined from the chronologically concentrated juveniles, in so far as they differ from the constants of the complete life range, are not to be taken as indicating that the growth curve changes sharply in direction as the juveniles enter adolescence.

With respect to the coefficient C, this is high in the Montana series,* since the specimens were weighed immediately after birth, while the Platteville, Pierre and San Patricio juveniles had long since lost their prenatal food accumulation.

Loss of Weight in Hibernation

A further investigation was made of the Platteville series to determine the effect of hibernation. The material was divided into groups by sexes and by seasons, with a further division between juveniles and adolescents-plus-adults at 400 mm. The equation constants for these groups are found to be as follows:

	<u>C</u>	<u>P</u>
Autumn adult males	513	3.09
Spring adult males	493	3.12
Autumn adult females	643	3.48
Spring adult females	618	3.51
Autumn juvenile males ^ø	257	2.26
Spring juvenile males ^ø	421	2.97
Autumn juvenile females ^ø	193	2.02
Spring juvenile females ^ø	260	2.59

From these figures it will be observed that the seasonal differences are quite marked. They result from the long period of abstinence from food during hibernation. The autumn form probably more nearly approaches the normal when the rattlers are feeding regularly, although they may be a little over-fat in preparation for their long prospective fast. But in the spring when issuing from hibernation, they are certainly thinner than during their active season in the summer.

The ratio of the spring to the autumn weight for each sex for any given length is indicated by the equation:

$$R = \frac{C_s L^P_s}{C_A L^P_A} = \frac{C_s}{C_A} L^{P_s - P_A}$$

* These Montana juvenile weights were kindly supplied to me by Dr. H.K. Gloyd.

^ø The separate seasonal constants of the juveniles, when combined, will not check exactly with the figures given in Table 15, since these separate figures were determined graphically. The spring juvenile constants are less accurate than those of autumn as there were fewer specimens in the former season.

But the values of P for each sex (in the adult class) are so nearly equal that the variability factor with L becomes unity, and the ratio of the coefficients gives the ratio of the weights with as close a degree of accuracy as is warranted by the character of the data. Thus, we find that at any length the spring adult males have 96.1 per cent of the weight of the autumn males, and the females 96.2 per cent; that is to say, the males lose 3.9 per cent and the females 3.8 of their initial autumn weight during hibernation. Amongst the juveniles, using their constants, we find the corresponding losses to be 29.6 per cent in the males and 34.6 per cent in the females.

These calculations are premised on one important, and possibly invalid, assumption, namely that the snakes do not increase in length during hibernation. As a check on this assumption, we first investigate the juveniles. The average length of the autumn specimens (160 in number) was 299 mm., while the average of the spring juveniles was 296 mm. (69 specimens). The difference represents a shrinkage rather than a growth, but as it is but one per cent, it may be assumed to be within the variations that are to be expected in the collection as a representative sample. We may therefore conclude that the juveniles are practically without increase in length during hibernation.

As the curves for the juveniles are of questionable accuracy as regards alignment, and the losses calculated from these curves, therefore, not as accurate as the adult calculations, some special weight determinations were made on groups of live juveniles of the Platteville series, giving averages more accurately than could be secured by weighing individual specimens or calculating from the doubtful curves. In the autumn 91 single-rattle individuals were found to average 13.04 g., while in the spring 40 snakes falling within this class weighed 9.97 g. each. The loss was 3.07 g. or 23.5 per cent of the autumn weight. Similarly, in the fall, 29 two-rattle juveniles averaged 17.72 g., while in the spring 10 specimens in this class weighed 14.15 g. each. Thus the loss was 3.57 g., or 20.1 per cent, and the single and two-rattle specimens show a fair agreement. Further, the two-rattle individuals made up 24.1 per cent of the autumn specimens and 20.0 per cent of the spring, therefore there is evident no tendency of individuals to advance from the single to the two-rattle class during hibernation. We may conclude that there is a loss of weight of somewhat in excess of 20 per cent in the juveniles during hibernation.

As the spring juvenile formulas have higher coefficients than the autumn, there is indicated a smaller per cent loss in weight of the larger specimens during hibernation, as compared with the smaller.

It is noted that the two sex curves of the juveniles cross each other in each season; that is to say, the smaller juvenile males are lighter than the females, while the larger males are heavier than the females of corresponding size, this being true both in spring and autumn. But these differences are relatively small considering the dispersion of individual specimens; sexual dimorphism in weight is of doubtful validity amongst the juveniles.

Returning to the adults, we have seen that if we

assume no growth in hibernation the formulas indicate a loss of weight of somewhat less than 4 per cent.

If, however, we assume some growth in the hibernating period the loss must be considerably less, for each individual is then advanced to a higher length-class in the spring and consequently works out to a greater weight by the formula.

We find from the statistics of length of all specimens over 400 mm. that the average male increases from 705 mm. in the autumn to 717 in the spring, a growth of 12 mm., and the average female from 665 mm. to 680 mm., or a growth of 15 mm.; the weighted average growth for the sexes combined is from 686 mm. to 698 mm., or 12 mm.

If we assume that these average growths, which are derived from measurements of 629 adolescent and adult specimens (206 spring, 423 autumn), are truly representative of the population, and that the situation which exists in nature has not been modified through the keeping of all specimens in captivity for about a month after their normal hibernation and dispersion dates, we should be forced to the conclusion, by determining from the formulas the weights which correspond to these average lengths, that the average male snake changes in weight from 174.2 g. to 174.0 g., a small loss; while the females (due to greater indicated growth in length) increase from 155.4 to 159.6 g., a gain of 2.7 per cent.

An increase in weight during hibernation cannot be possible, since the animals are without food, and are presumed to be practically dormant. We are therefore led to believe that the increase in length which is indicated in the females does not really occur in nature, the apparent increase being the result of the extra month in captivity and the exigencies of sampling. Reviewing all the data available for both juveniles and adults, we reach the conclusion that there is no growth in length during hibernation, and that the loss in weight during this period approximates 4 per cent in adults, and somewhat over 20 per cent in the juveniles.

It may be stated that the juvenile specimens were kept a shorter time between the collecting date and date of measurement than the adults, which might explain the smaller seasonal difference in the average size of the juveniles. It should be understood that specimens were given water but no food during this period of captivity.

If loss in weight were proportional to surface area and 22.7 per cent is the loss in the juveniles (this is the weighted average found above) then the loss of a 700 mm. adult would be 9.7 per cent, a considerably higher result than is obtained by the other method of computation. Thus, if most of the loss results from radiation, it is not proportional to surface area; this would be expected if the snakes ball-up in hibernating.

It may be of interest to record the growth of 5 adult specimens retained in captivity over one winter. Although offered food they did not eat well, as is usually the case with rattlers in captivity. They gained an average of 2.5 per cent in length but at the same time lost no

less than 35 per cent in weight. Of course the conditions surrounding these specimens during their winter of captivity were quite different from those affecting snakes in hibernation, for the former were kept at household temperatures and remained active throughout the period.

Conclusions:

1. Studies of rattlesnake growth cannot be based on captive specimens, since growth is distorted by artificial conditions. Skins should not be used as indicators of rattlesnake length because of stretching in preservation.

2. Extent of dispersion in body length: The coefficient of variation of length in a brood of young rattlesnakes at birth averages about 3.5 per cent. Groups of young from the same area run 5 per cent at birth in late summer, and diverge to 8 per cent at the time of hibernation. At the age of 8 months this dispersion has increased to about 10 or 12 per cent. A homogeneous adult and sub-adult population is found to have a coefficient of variation of 15 per cent. Purely adult populations are difficult to segregate but probably run from 8 to 14 per cent.

3. Character of dispersion in length: In size distribution a group of young rattlesnakes, from one area, but born of several mothers, follows the normal curve of error. Extreme variants are more often stunted than oversize. There are indications that throughout life, the dispersion curve for each age-class remains normal. However, because dispersion in length increases, it is impossible to segregate age-classes after the first year. Complete adult populations are platykurtic in size-class distribution.

4. Sexual dimorphism in body length: At birth male rattlesnakes average one per cent longer than females. This increases to about 3 per cent in the following spring. In a composite population of adolescents and adults the male superiority is 5 per cent. Sexual dimorphism becomes accentuated after the snakes are $1\frac{1}{2}$ years old. In an adult population the males average 10 to 12 per cent longer than the females. The longest specimens are always males, and in any species the longest (rather than the average) males are about 15 per cent longer than the corresponding females. C. cerastes is a conspicuous exception to the rule of male superiority; in this species the adult females are about 5 per cent longer than the males.

5. A summary is presented of the average growth of one subspecies of rattlesnake, C.v. oreganus, derived with considerable accuracy during its first year of life, and somewhat less during the second. Young rattlesnakes are born in the early autumn, in most areas in September or early October. Females go into their third